Université Montpellier II Sciences et Techniques du Languedoc

Ecole Doctorale : Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosciences, Environnement (SIBAGHE)

Dossier présenté pour l'obtention
de l'**Habilitation à Diriger des Recherches**

par
Geo Coppens d'Eeckenbrugge

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Le 27 mai 2013

Mesdames Nathalie Charbonnel et
Christine Chevillon
Ecole Doctorale SIBAGHE

Mesdames,

Veuillez trouver ci-joint mon dossier de candidature à la soutenance d'une habilitation à diriger des recherches, pour validation. Je n'ai formulé aucune demande auprès d'une autre université.

Dans la notice jointe, la synthèse de mes recherches est essentiellement centrée sur le thème de la **diversité génétique et domestication des fruitiers néotropicaux.** A partir de mon expérience sur les plantes pérennes américaines, elle ouvre sur mon projet de recherche sur les interactions homme-société, portant l'accent sur la **structuration sociale de l'agrobiodiversité et sa distribution**.

Pour le jury, je vous soumets la proposition suivante :

Rapporteurs :

Prof. **Laurent Legendre** (physiologie, botanique), Université de Saint Etienne (notamment pour son intérêt pour la domestication et la sélection des racines et tubercules).

Dr. **Thierry Robert** (HDR), du Laboratoire Ecologie, Systématique et Evolution, de l'Université Paris-Sud

Dr. **Yves Vigouroux** (HDR), UMR Diversité Adaptation et Développement des plantes (DIADE, Montpellier), inscrit à l'ED SIBAGHE.

Examinateurs :

Prof. **Patrick Van Damme**, du Laboratoire d'Agriculture et Ethnobotanique Tropicale et Subtropicale, de l'Université de Gand.

Dr. **Joëlle Ronfort** (HDR), UMR Amélioration Génétique et Adaptation des Plantes méditerranéennes et tropicales (AGAP, Montpellier), inscrite à l'ED SIBAGHE.

En vous remerciant de l'attention que l'école doctorale voudra bien porter à ma requête, je vous prie d'agréer, Mesdames, l'assurance de ma considération distinguée.

Coordonnées des membres proposés pour le jury

Rapporteurs

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Montpellier, le 25 mai 2013

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Candidature HDR /Geo Coppens d'Eeckenbrugge

Monsieur le Président
Université Montpellier II

Monsieur le Président,

Nous vous prions de bien vouloir trouver ci-joint le dossier de candidature à l'habilitation à diriger des recherches de Géo Coppens d'Eeckenbrugge, actuellement chercheur CIRAD, accueilli au Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175) dans l'équipe Interactions bioculturelles.

Géo Coppens d'Eeckenbrugge est agronome et sélectionneur de formation. Ses recherches, initialement tournées vers la génétique et l'amélioration des plantes, se sont progressivement orientées vers l'étude de la variabilité génétique et morphologique de différentes espèces cultivées et pérennes, tropicales et néo-tropicales. Plus récemment, et en intégrant, à ses études, des concepts et outils issus des sciences sociales, Géo Coppens d'Eeckenbrugge a ré-orienté ses recherches sur l'étude de l'évolution des plantes cultivées. Son projet de recherche, original et ambitieux, vise ainsi à mieux comprendre les processus de domestication des espèces néo-tropicales pérennes en prenant en compte les contextes culturels et historiques dans lesquels ces domestications ont eu lieu. A travers le lien qu'il implique entre les disciplines de la biologie évolutive, des sciences sociales et de l'étude des plantes cultivées, ce projet s'insère particulièrement bien dans le tissu scientifique montpelliérain. Par ailleurs, peu d'étude sur les processus de domestication ont considéré le cas des plantes pérennes ; le projet de recherche proposé par Géo Coppens d'Eeckenbrugge devrait donc contribuer de façon originale à une meilleure compréhension des processus de domestication. Les domaines de compétences de Géo Coppens d'Eeckenbrugge incluent entre autres la génétique et l'amélioration des plantes, la biogéographie, la génétique quantitative, la cyto-génétique et les approches SIG. Le dossier scientifique de Géo Coppens d'Eeckenbrugge remplit largement les conditions nationales reconnues dans sa discipline pour l'obtention de l'HDR :

- il a soutenu sa thèse de doctorat en 1987

- il est auteur de 27 articles parus dans des revues internationales référencées, de 51 publications dans des revues non indexées, d'un livre et de 27 chapitres de livres ou monographies. Il a également été éditeur des actes d'une conférence et il est l'auteur principal de nombreux rapports scientifiques. Il est co-auteur d'une soixantaine de communications données en conférences nationales et internationales, parmi lesquelles 23 associent des étudiants encadrés.

- il a co-encadré les recherches de quatre doctorants. Il a dirigé le travail de neuf étudiants en dernière année d'école d'ingénieurs, de cinq étudiants en master, et d'un étudiant de licence.

- Onze de ses articles publiés dans des revues indexées sont co-signés avec un ou plusieurs étudiants. Quatorze des 51 publications non indexées et trois des 27 chapitres de livres/monographies incluent également des étudiants.

- Il a rédigé et coordonné quatre programmes scientifiques internationaux dont un projet EU-INCO (1997-2001), un projet Colciencias, Colombie (1999-2001), un projet FONTAGRO, Amérique du Sud (1999-2003), et un projet financé par le ministère de l'environnement colombien (2003-2005).

- La reconnaissance par ses pairs tant de ses compétences scientifiques que de ses qualités pédagogiques s'est notamment traduite par son activité d'évaluateur scientifique pour de nombreuses revues et pour le site internet de la base de données des espèces invasives, par son rôle d'éditeur associé de la revue *Revista Brasileira de Fruticultura*, et par son rôle de coorganisateur du congrès international d'ethnobiologie en 2012.

Par ailleurs, le directeur de l'ED n'a constaté aucun problème. Au bilan, le bureau de l'ED SIBAGHE a donc exprimé **une appréciation favorable** sur ce dossier HDR.

Nous proposons les trois rapporteurs suivants pour l'évaluation de ce dossier d'HDR:

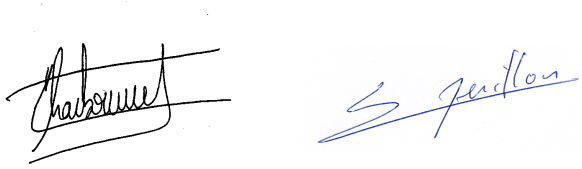
1- Pr. Laurent Legendre, Université Jean Monnet à Saint Etienne, UFR des Sciences et Techniques. Villeurbanne.
2- Dr. Thierry Robert (HDR), Laboratoire Ecologie, Systématique et Evolution de l'Université Paris-Sud XI.
3- Dr. Yves Vigouroux (HDR), UMR DiADE à Montpellier, représentant de l'ED Sibaghe

Pour compléter le jury, en plus des trois rapporteurs, nous proposons de nommer comme examinateurs les personnalités suivantes :

4- Pr. Patrick Van Damme, Laboratory for Tropical and Subtropical Agriculture and Ethnobotany. Université de Gand, Belgique.
5- Dr. Joëlle Ronfort (HDR), UMR AGAP à Montpellier.

Nous vous prions d'agréer, Monsieur le Président, l'expression de nos respectueuses salutations.

Nathalie Charbonnel et Christine Chevillon pour l'ED SIBAGHE



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Montpellier, le 28 mai 2013

A l'attention de l'Ecole Doctorale SIBAGHE

Objet : Candidature à l'Habilitation à Diriger des Recherches (HDR) – Geo COPPENS

Madame, Monsieur,

Arrivé au CEFE en janvier 2005, comme membre de l'UR 67 du CIRAD, Geo Coppens est devenu membre de l'équipe Interactions Bioculturelles de l'UMR CEFE 5175 en 2007. Les objectifs de cette équipe sont (1) comprendre les dynamiques sociales et biologiques responsables de l'origine et du maintien de la diversité culturelle et biologique que représentent les ressources génétiques cultivées, ainsi que de toute autre forme de biodiversité associée, et (2) de développer des méthodes originales de co-construction entre, d'une part, les disciplines de sciences humaines et sciences du vivant et, d'autre part, entre chercheurs et acteurs locaux en vue d'une gestion *in situ* durable associant conservation et valorisation.

Geo Coppens a contribué aux études sur l'agrobiodiversité, en Amérique tropicale et en Afrique equatoriale, par la poursuite de ses travaux sur les passiflores, notamment en Colombie et en Guyane, et par une étude phylogénétique du safou (*Dacryodes edulis*) et des espèces apparentées au Cameroun et au Gabon. Il développe des études sur les relations entre distribution géographique des espèces et leur domestication (cacao, avocat, coton) en lien avec des données linguistiques.

Au cours de ses recherches, Geo Coppens a contribué à la formation d'étudiants en master et en thèse, par la direction de stages (trois), le co-encadrement de thèses (deux), ou encore la participation à des modules de formation (projet GUYAMAZ de formation sur la domestication et la diffusion des plantes amazoniennes). J'émets donc un avis très favorable sur le travail fourni par Geo Coppens dans le cadre de la rédaction de son HDR.

Je vous prie de croire, Madame, Monsieur, à l'expression de mes salutations distinguées.

CENTRE NATIONAL DE LA RECHERCHE SCIENTIFIQUE
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CENTRE D'ÉCOLOGIE FONCTIONNELLE ET ÉVOLUTIVE

Le Directeur Adjoint
p.o
Richard JOFFRE
Directeur de Recherche CNRS
Philippe JARNE

Université Montpellier II Sciences et Techniques du Languedoc

Ecole Doctorale : Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosciences, Environnement (SIBAGHE)

DIVERSITE GENETIQUE ET DOMESTICATION DES FRUITIERS NEOTROPICAUX

Synthèse de travaux présentée pour l'obtention
de l'**Habilitation à Diriger des Recherches**

par
Geo Coppens d'Eeckenbrugge

Diversité génétique et domestication des fruitiers néotropicaux

1. Un parcours en trois phases

2. Ressources génétiques et domestication des plantes fruitières pérennes – Synthèse sur trois groupes néotropicaux ...……..7

1. Un parcours en trois phases

Agronome "tropicaliste" et sélectionneur de formation, ma carrière au CIRAD m'a amené à me spécialiser dans les ressources génétiques des fruitiers néotropicaux. Incluant plus de 1200 espèces, cette richesse est particulièrement développée aux Amériques, et doit être située à la fois dans un contexte général de biodiversité extrême et des effets de modes de gestion très diversifiés, enracinés dans des civilisations très anciennes et originales. Mon intérêt pour les mécanismes qui ont abouti à la transformation, voire la domestication, de tant d'espèces ayant un cycle de vie souvent aussi long que les hommes des sociétés qui les ont exploitées, m'a conduit à intégrer l'équipe "interactions bioculturelles", dont je fais actuellement partie au CEFE.

Mais avant d'en arriver là, il me faut reprendre brièvement au début la séquence d'activités de recherches qui aboutit à présenter ma candidature à une HDR aujourd'hui. D'un point de vue thématique général, on peut découper mon parcours de chercheur selon trois phases, correspondant à trois domaines : génétique et amélioration des plantes, ressources génétiques des fruitiers américains, et interactions bioculturelles. Dans le présent document, la synthèse de mes travaux portera essentiellement sur la seconde phase (ressources génétiques des fruitiers américains), en reconsidérant ses résultats du point de vue de la domestication des plantes pérennes, tandis que la description de mon projet de recherche portera sur la troisième phase, examinant les interactions plantes-sociétés sous un angle plus large, incluant l'évolution sous culture et/ou sous domestication, les facteurs sociaux qui la déterminent (relation entre diversité sociale et diversité génétique) et inversement l'impact de la domestication des plantes sur l'évolution des sociétés.

1.1. Génétique et amélioration des plantes

Dès l'obtention de mon premier diplôme, en 1981, j'ai intégré une équipe de recherche d'amélioration de la chicorée de Bruxelles (*Cichorium intybus* L.) au Laboratoire de Phytotechnie Tropicale de l'Université Catholique de Louvain. J'y étais chargé plus particulièrement d'en étudier le système de reproduction. C'est ainsi que j'ai pu développer ma thèse doctorale sur les relations pollen-pistil, centrée sur les phénomènes d'auto-incompatibilité, d'interactions entre pollens compatibles et incompatibles, de compétition gamétique, et sur leur déterminisme génétique. Parallèlement, j'étais affecté au suivi du programme de sélection qui était développé par un institut de recherche agronomique voisin, à Gembloux, et j'avais donc l'occasion de mettre en application mes propres résultats (les génotypes étudiés pour ma thèse provenant des géniteurs du programme de création variétale). J'eus d'ailleurs très rapidement l'occasion de les appliquer au sein du tout premier programme pour le développement de chicorée à inuline à partir de variétés de chicorée à café, programme dont j'ai coordonné la partie génétique et la sélection pendant ses trois premières années. Ce programme a par la suite brillamment réussi, puisqu'il a permis une diversification des zones betteravières dans une région sucrière répartie entre la France et la Belgique (Nord, Ardennes, Wallonie).

Les recherches menées au Laboratoire de Phytotechnie Tropicale m'ont donné l'occasion d'aborder d'autres espèces, notamment à travers l'encadrement des travaux de fin d'étude d'étudiants en agronomie. C'est ainsi que je me suis intéressé aux incompatibilités intra et interspécifiques dans le genre *Brachiaria* (graminées fourragères tropicales) et que deux de ces étudiants ont pu montrer le lien génétique étroit entre sexualité et auto-incompatibilité d'une part et apomixie/pseudogamie et auto-compatibilité d'autre part.

Engagé au CIRAD en 1989 et affecté en Martinique jusqu'en 1994, j'ai poursuivi des travaux analogues sur l'ananas, mêlant l'étude de sa biologie de la reproduction (évolution de la fertilité en relation avec la domestication, phénomènes d'auto-incompatibilité), développement de stratégies de sélection et création variétale (introduction de phases de consanguinisation dans les schémas de croisement). En même temps, j'ai eu l'occasion de participer significativement aux travaux de collecte et caractérisation des ressources génétiques, dans le cadre d'un projet européen porté par l'équipe ananas du CIRAD, ce qui m'a donné une expérience déterminante pour la seconde phase de mon parcours.

1.2. Ressources génétiques des fruitiers néotropicaux

Affecté au bureau Amériques de l'IPGRI (actuellement Bioversity International) de 1994 à 2002, j'ai pris en charge la coordination internationale des réseaux éco-régionaux REDARFIT (Réseau Andin de ressources phytogénétiques) et TROPIGEN (ressources génétiques amazoniennes). Outre cette coordination, et en fonction des priorités dégagées au sein de ces réseaux régionaux, je me suis intéressé plus particulièrement aux passiflores et aux Caricaceae, en suscitant et soumettant des projets nationaux et régionaux, auxquels je participais ensuite comme coordinateur et comme chercheur, en m'impliquant directement sur un des volets. Outre les chercheurs nationaux, ma recherche sur ces deux groupes de fruitiers impliquait directement des étudiants de tous niveaux, du stage libre jusqu'au doctorat, ainsi qu'une post-doctorante. Je gardais en outre une activité sur l'ananas, par le montage, la soumission puis la coordination d'un second projet européen impliquant des institutions de France (CIRAD), du Portugal (U. do Algarve), du Venezuela (U. Maracay et FONAIAP) et du Brésil (EMBRAPA). Enfin, j'assurais un suivi général sur la diversité des fruitiers américains, afin de pouvoir répondre aux sollicitations des programmes nationaux de ressources génétiques en la matière.

Dans une région caractérisée par une biodiversité particulièrement élevée, tant dans les écosystèmes "naturels" que dans les systèmes agricoles ou agroforestiers, le premier travail est un inventaire de la richesse exploitée (plantes cultivées ou gérées "in situ") ou disponible à l'état spontané. Cela se traduit par un investissement important dans la systématique, aux niveaux intra- et interspécifiques. Les travaux de caractérisation phénotypique et génétique visent souvent à valider ou corriger les classifications existantes. C'est ainsi que j'ai été amené à décrire une espèce de passiflore andine, pourtant cultivée sur des milliers d'hectares, à réexaminer les relations entre différentes passiflores ou papayes, ou à proposer une classification simplifiée du genre *Ananas*.

Les travaux sur passiflores et papayes de montagne ont également été mis à profit pour une étude de distribution géographique de leur diversité, en les utilisant comme groupes représentatifs des nombreux taxons qui ont connu une radiation récente liée au soulèvement andin. Ainsi, outre la connaissance des ressources génétiques des passiflores et papayes de montagne en elles-mêmes, un objectif important de cette étude était d'utiliser ces espèces comme indicateurs dans une cartographie de la biodiversité de la zone caféière colombienne au moyen d'un système d'information géographique. L'étude a notamment montré une correspondance frappante entre la distribution de certains écotopes des paysages caféiers et les aires de richesse spécifique maximale. Au-delà de leur intérêt académique et pratique, pour la gestion environnementale de la région caféière, ces études m'ont convaincu de l'utilité des Systèmes d'Information Géographique pour la modélisation de niches écoclimatiques, en complément de la caractérisation morphologique et/ou génétique.

Enfin, ces travaux sur Passifloraceae et Caricaceae ont donné lieu à de nombreux travaux d'étudiants, surtout français et colombiens. L'un d'eux, John Ocampo, a poursuivi ses études postgraduées en France, obtenant successivement un DEA et un doctorat (co-encadré avec Philippe Feldmann).

1.3. Interactions bioculturelles : domestication, structuration sociale des ressources génétiques, anciens systèmes agro-forestiers d'Amérique tropicale

Peu après mon retour d'expatriation, en 2005, j'ai intégré l'unité de recherche 67 "gestion des ressources génétiques et dynamiques sociales" du CIRAD. Cette unité a été dissoute et reformée dans une équipe du CEFE, nommée "interactions bioculturelles" et intégrant des collègues du CNRS, de l'IRD et de l'Université.

J'ai dû reconsidérer les thèmes de recherches sur passiflores, papayes et l'ananas, notamment en fonction des possibilités d'accès au terrain. Pour les papayes et les ananas, la recherche s'est limitée à la valorisation des données acquises antérieurement, tout en centrant la réflexion sur les aspects de domestication. Quant aux passiflores, la thèse de John Ocampo s'est terminée en 2007. Ses résultats ont montré une évolution réticulée dans le genre, marqueurs morphologiques, chloroplastiques, mitochondriaux et nucléaires produisant des phylogénies très divergentes. Le problème des relations entre espèces et de leur potentiel pour l'amélioration ou la substitution des cultigènes ne pouvait donc être considéré à partir d'une approche classificatoire "top-down". La logique de l'approche a été inversée, en partant de groupes d'espèces particulièrement homogènes dans leur morphologie et dans leur écologie. Elle a commencé à être appliquée en Guyane, sur les groupes des *Laurifoliae* (passiflores à fort potentiel fruitier) et de l'ancien sous-genre *Distephana* (passiflores à fleurs rouges des forêts humides de basse altitude). Au-delà des aspects systématiques traditionnels, se posent la question des facteurs déterminant la radiation spécifique dans un environnement apparemment homogène, ainsi que la question de la domestication de certaines espèces. Par exemple, pourquoi l'espèce cultivée aux Antilles est-elle essentiellement sauvage en Guyane, où une autre espèce du même groupe morphologique est cultivée ?

Plusieurs recherches de l'équipe se situant en Afrique, je me suis intéressé au safoutier (*Dacryodes edulis*), espèce qui, selon Chevalier (1916), est probablement le seul arbre fruitier indigène "vraiment cultivé par les indigènes du bassin du Congo et de tout le Gabon, et cette culture a dû prendre naissance à une époque très reculée». Le genre pantropical *Dacryodes* compte une vingtaine d'espèces africaines. Le projet ANR IFORA m'a permis, dans le cadre d'une étude phylogéographique centrée autour des massifs forestiers du Cameroun et du Gabon, de m'intéresser aux relations entre le safou cultivé et les populations sylvestres, tant de *D. edulis* que d'autres espèces proches. Ce travail est mené en collaboration étroite avec Gilbert Todou, enseignant-chercheur à l'Ecole Nationale Supérieure à Maroua (Cameroun).

Dans le cadre initial de l'unité 67, la collaboration avec Fabrice Sagnard, généticien spécialisé notamment sur le sorgho, et Christian Leclerc, anthropologue, a débouché sur le montage d'un projet ATP-CIRAD intitulé "Reproduire une plante, reproduire une société", sous la coordination de Christian Leclerc. L'hypothèse de travail est que, dans les sociétés traditionnelles, les échanges de semences prennent place très préférentiellement au sein de réseaux sociaux préexistants, essentiellement structurés selon les règles de filiation, héritage, mariage. Un autre niveau de structuration a priori important est lié à la différenciation linguistique. Le projet ATP vise à étudier les conséquences de la différenciation sociale des agriculteurs sur l'organisation de la diversité de leurs ressources génétiques de sorgho, chez les Meru vivant sur les pentes orientales du Mont Kenya. Ma contribution s'est située essentiellement dans l'élaboration d'un corpus théorique à l'interface entre l'anthropologie sociale et la génétique des populations cultivées. Ce travail a été important dans la phase de montage du projet, avant le travail de terrain, et, après celui-ci, dans la phase d'analyse et d'interprétation, encore en cours. Un article de synthèse sur l'impact des facteurs sociaux sur la diversité des plantes cultivées, co-rédigé avec Christian Leclerc, en est le premier aboutissement important.

Une collaboration a également été engagée avec Cecil Brown, un linguiste américain, intéressé par une lecture bi-directionnelle des relations entre plantes et sociétés du passé, à travers le prisme de la méthode de linguistique comparative. Cecil Brown (2010) a étudié la reconstruction des noms de 30 espèces, parmi les plus largement utilisées par les civilisations mésoaméricaines. La composition du portefeuille d'espèces propre à chaque groupe linguistique permet de reconstituer son habitat passé, par le biais de la modélisation des niches écoclimatiques de ces espèces. La méthode est testée sur la famille Otomangue et sa branche zapotèque, dont la localisation géographique actuelle, relativement bien circonscrite, devrait faciliter l'interprétation des résultats.

Parallèlement, l'étude des niches écoclimatiques de certaines espèces peut être développée pour elle-même, notamment lorsque l'exercice de modélisation permet de mieux comprendre les relations entre populations sauvages et cultivées, ce qui conduit alors directement à des questions sur l'origine et la domestication des cultigènes et sur la relation entre la distibution originelle et l'aire de culture.

2. Ressources génétiques et domestication des plantes fruitières pérennes – Synthèse sur trois groupes néotropicaux

Mes recherches sur les ressources génétiques des fruitiers tropicaux se sont développées dans un contexte de recherche appliquée, organisée par filières de production, et essentiellement financée sur projets. Bien que la problématique de la domestication n'y fût pas centrale, nombre de leurs résultats ont pu être réexaminés sous cet angle particulier. Chacun des groupes de plantes, présentant une évolution propre, sera traité séparément. Je ne traiterai pas ici de mes expériences antérieures à 1989, concernant la chicorée et une plante fourragère tropicale, *Brachiaria ruziziensis*.

2.0. Quelques définitions préliminaires

Dans une révision récente sur les processus de domestication au Proche Orient, Abbo et al. (2012) soulignent l'importance de la définition des termes utilisés dans la description des liens entre hommes et plantes (culture, domestication, agriculture, production de nourriture), citant Harris (1989) : "the meaning attributed to such general concepts can and do directly affect reserarch design and the interpretation of evidence".

De plus en plus, la domestication est étudiée comme un processus de co-évolution par lequel la sélection humaine, consciente ou inconsciente, modifie les phénotypes et génotypes des plantes tolérées, favorisées, propagées ou cultivées. Le degré de modification peut varier entre espèces et entre populations d'une même espèce. C'est ainsi que Clement et al. (2010)[1] considèrent quatre niveaux : "wild", "incipiently domesticated", "semi-domesticated" et "domesticated". Les populations de cette dernière catégorie ont perdu leurs adaptations originales leur permettant de se perpétuer hors de l'influence humaine, adaptations qui touchent particulièrement leurs capacités de survie et de propagation (Clement et al., 2010).

Le processus de domestication peut aboutir à la formation d'une nouvelle espèce, par exemple le guaraná (*Paullinia cupana* Kunth), un fruitier amazonien allopolyploïde. On a dès lors un cultigène, au sens de la définition de Bailey de 1923 : " a species, or its equivalent, that has appeared under domestication…". La première définition, de 1918, se référait à des espèces ou groupes (taxonomiques). Elle semble mieux adaptée à la nomenclature actuelle, qui favorise le replacement des cultigènes au sein de leur espèce d'origine. On peut alors définir le cultigène comme un taxon issu de la domestication. Le premier exemple de Bailey, le maïs, reste donc un cultigène, même s'il n'est maintenant considéré que comme une sous-espèce de la téosinte.

Comme toute évolution, la domestication est liée à la sélection, consciente ou non, mais l'inverse n'est pas toujours vrai. La diversité des situations est particulièrement importante chez les plantes cultivées perennes. L'étude de la domestication impose de distinguer

[1] Les références en bleu se rapportent à des articles écrits ou co-écrits par le candidat.

l'ensemble des caractères décisifs qui forment le syndrome de domestication de ceux qui ont pu évoluer avant ou après la domestication. Cette question est particulièrement importante dans le débat actuel sur la durée de la domestication des céréales (cfr. modèle dit de "protracted domestication").

2.1. Ananas

L'ananas, *Ananas comosus* var. *comosus*, est la seule Broméliacée d'importance économique mondiale. Cultivé dans toutes les régions chaudes, il constitue la troisième production fruitière tropicale, derrière la banane et l'avocat (l'orange étant considérée subtropicale). Sa propagation végétative par différents types de rejets, y compris la couronne du fruit composé, est aisée, et les cultivars sont donc des clones, bien que la reproduction sexuée reste fonctionnelle et utilisable pour l'amélioration génétique. L'existence d'un système d'auto-incompatibilité gamétophytique, combinée à la parthénocarpie de l'espèce, permet l'obtention de fruits aspermes en culture monoclonale et/ou en absence de colibris, pollinisateurs naturels de l'espèce.

La diffusion pantropicale de l'ananas a été fulgurante, puisqu'elle a essentiellement eu lieu sur un siècle, à partir de la première observation du fruit par Christophe Colomb lui-même, en 1493. Son adoption par les horticulteurs du monde entier a été telle que certains botanistes l'ont décrit comme originaire d'Asie ou d'Océanie. Les premières descriptions des conquérants espagnols attestent par ailleurs que cette *success story* était déjà ancienne, puisque la culture de l'ananas était déjà largement répandue dans toute l'Amérique tropicale. Quatre siècles plus tard, le développement des conserveries conféra à la culture une image liée aux grandes plantations et à l'industrie, masquant la réalité d'une production mondiale essentiellement tournée vers la satisfaction des besoins et marchés locaux. Parallèlement, l'écrasante prépondérance d'un seul cultivar dans la grande majorité des plantations "industrielles" masquait l'existence d'une grande diversité génétique encore disponible en Amérique du Sud (Rohrbach et al., 2003).

Ainsi, pendant un siècle, la base des travaux d'amélioration, et des études génétiques associées est restée limitée à cinq "groupes" variétaux, dont quatre correspondaient à des clones ou paires de clones. Dans le même temps, le nombre d'espèces d'ananas était revu à la hausse, passant de une ou deux espèces, selon les classifications du début du XXe siècle, à huit espèces réparties en deux genres, *Ananas* et *Pseudananas*, selon la classification de Smith et Downs (1979). Six de ces espèces étaient souvent considérées comme sauvages. Cette situation était liée à une connaissance très incomplète des aires de distribution et de culture traditionnelle aux Amériques, notamment une négligence de la diversité existant au Nord de l'Amérique du Sud, dans les bassins de l'Amazone et de l'Orénoque, et à une approche taxonomique volontairement restreinte à l'étude en herbiers (Leal et al., 1998).

Pourtant, Brücher (1971) avait rapporté l'existence de formes sauvages dans les bassins de l'Orénoque et du Ventuari, suggérant qu'une domestication de l'ananas était aussi plausible au Nord qu'au Sud de l'Amazonie. Mais ce sont les inventaires du Professeur Leal (U. Central de Venezuela) qui permettent pour la première fois de défendre l'idée de l'existence d'une plus grande diversité au Nord de l'Amazone, tant pour l'ananas sauvage que cultivé. Et c'est au Venezuela, cinquante ans après l'exploration du Sud du continent par des chercheurs Etats-Uniens, que reprendront les collectes systématiques de germoplasme d'ananas, dans le cadre d'une collaboration entre l'U.C.V. et le CIRAD (Leal et al., 1986). Peu après, le programme d'amélioration et la collection vivante du CIRAD étaient transférés en Martinique et deux généticiens (moi-même en 1989 et Marie-France Duval en 1990) étaient chargés de la sélection en cours et de l'étude des nouvelles introductions. Nous avons travaillé en tandem, Marie-France se consacrant d'avantage à la caractérisation morphologique et génétique et moi-même à la biologie de la reproduction et aux méthodes de sélection. Un important programme de collecte fut engagé, dans le cadre d'un premier projet européen. En collaboration avec nos collègues brésiliens, furent prospectés tour à tour l'Amapa, le cours supérieur de l'Amazone (Rio Solimões), le cours du Rio Negro, l'Acre et le Nord du Mato Grosso, les états du Sud du Brésil, et la Guyane Française (Figure 1), enrichissant les collections brésilienne et française de centaines d'accessions et élargissant considérablement nos connaissances de terrain (Duval et al., 1997 ; Coppens d'Eeckenbrugge et al., 2002 ; Ferreira et al., 2005). L'étude de ces matériels a été approfondie par l'obtention d'un second financement européen, comprenant un important volet de génétique moléculaire mis en œuvre par Marie-France Duval, à l'occasion d'un projet que j'ai coordonné depuis mon affectation en poste à l'IPGRI-Amériques. L'ensemble de ces observations allait nous amener à reconsidérer la taxonomie de l'ananas et émettre de nouvelles hypothèses sur sa domestication.

Alors que certains auteurs (e.g. Pickersgill, 1976) opposaient l'auto-incompatibilité de l'ananas cultivé et l'autocompatibilité des formes sauvages, notre étude de la reproduction sexuée dans le genre *Ananas sensu* Smith & Downs n'a pas permis d'établir une telle différence qualitative. La distribution de la fertilité et de l'autofertilité montre (1) une certaine continuité entre ces formes et (2) que l'effet du système d'auto-incompatibilité est plus ou moins fortement atténué chez de nombreux clones (pseudo-autocompatibilité), permettant parfois une autofertilité non négligeable. Cependant, la fertilité est généralement plus faible dans la forme cultivée pour le fruit que dans les formes sauvages ou cultivées pour la fibre. Le phénomène de pseudo-autocompatibilité est également plus fréquent dans les formes sauvages ou cultivées pour la fibre ou en haie vive. Cette distribution, ainsi que la corrélation entre fertilité d'une part, et quantité et viabilité du pollen d'autre part, indique que la domestication a (1) diminué la pression de sélection naturelle sur la régulation de la méiose, en renforçant le rôle de la reproduction végétative au détriment de la reproduction sexuée, et (2) instauré une pression de sélection artificielle contre la présence de trop nombreuses graines dans le fruit. Cette sélection artificielle a également abouti à augmenter la fréquence de clones fortement auto-incompatibles dans le matériel cultivé pour le fruit (Coppens d'Eeckenbrugge et al., 1993).

Figure 1. Zones prospectées en collaboration entre le CIRAD et l'EMBRAPA dans le cadre du premier projet européen (ellipses bleues) et principales prospections antérieures (ellipses rose orangé), au Vénézuéla (UCV-CIRAD) et au Pérou (INIA-CIRAD). L'étude moléculaire de Duval et al. (2003) a également porté sur un échantillon d'accessions de l'EMBRAPA collectées dans d'autres régions du Brésil.

Par ailleurs, nos observations sur les nombreuses descendances hybrides "interspécifiques" obtenues en Martinique n'ont montré aucune discontinuité dans la distribution des caractères morphologiques. L'observation de nombreux phénotypes intermédiaires lors des collectes confirme la continuité de la variation entre les formes diploïdes décrites, et seul *Pseudananas sagenarius* (syn. *Ananas macrodontes*), une forme tétraploïde autofertile rencontrée dans le Sud-Est du continent (forêt atlantique au Brésil et bassin du fleuve Paraná ; voir Figure 3), montre des caractères distinctifs (absence générale de couronne sur le fruit, reproduction végétative par stolons). L'étude

de la diversité des marqueurs enzymatiques (Aradhya et al. 1994) et, surtout, des marqueurs RFLP (Duval et al., 2001) a montré une faible différenciation entre les genres *Ananas* et *Pseudananas* de Smith & Downs. Au sein du premier, les limites interspécifiques n'étaient pas validées, la variation apparaissant plutôt continue, notamment entre les deux principales formes cultivées et la forme sauvage la plus répandue.

Cette analyse, affinée lors de la rédaction d'une série de chapitres d'ouvrages, initiée par le Prof. Leal (Leal et Coppens d'Eeckenbrugge, 1996 ; Coppens d'Eeckenbrugge et al., 1997 a, b), nous a amené à réviser et remettre en question la taxonomie de l'ananas (Leal et al., 1998), puis à proposer une classification simplifiée, réduisant les deux genres de Smith & Down à deux espèces, en restaurant l'espèce *A. macrodontes* Morren, tétraploïde, et en regroupant tous les diploïdes, tant sauvages que cultivés, sous *A. comosus*, les sept espèces diploïdes devenant cinq variétés botaniques (Tableau 1 et Figure 2; Coppens d'Eeckenbrugge et Leal, 2003).

Tableau 1. Correspondance entre la classification actuelle (Coppens d'Eeckenbrugge et Leal, 2003) et la précédente (Smith et Downs, 1979).

Coppens et Leal (2003)	Smith et Downs (1979)
***Ananas comosus* (L.) Merril**	
A. comosus var. *ananassoides* (Baker) Coppens & Leal	*A. ananassoides* (Baker) L.B. Smith *A. nanus* (L.B. Smith) L.B. Smith
A. comosus var. *erectifolius* (L.B. Smith) Coppens & Leal	*A. lucidus* Miller
A. comosus var. *parguazensis* (Camargo & L.B. Smith) Coppens & Leal	*A. parguazensis* Camargo & L.B. Smith
A. comosus var. *comosus*	*A. comosus* (L.) Merrill
Invalid (Leal 1990)	*A. monstrosus*
A. comosus var. *bracteatus* (Lindl.) Coppens & Leal	*A. bracteatus* (Lindley) Schultes f.
***Ananas macrodontes* Morren**	*Pseudananas sagenarius* (Arruda da Câmara) Camargo

Figure 2. En haut : principales caractéristiques distinctives d'*Ananas macrodontes** (espèce sauvage exploitée pour la fibre) : absence de couronne sur l'inflorescence, longues bractées florales, présence d'épines rétrorses et reproduction végétative par stolons. Au milieu : variation morphologique chez *A. comosus* var. *ananassoides* : petits plants et fruits en conditions forestières, relativement gros fruits collectés sur une savane-roche, et type intermédiaire, semi-domestiqué, dans un jardin de case (Guyane Française). En bas : *A. comosus* var. *parguazensis* (forme sauvage, *A.comosus* var. *erectifolius** (cultivé pour la fibre ou l'ornement), et *A. comosus* var. *bracteatus** (haie vive ou jardin).
* : photographies Garth Sanewski

La distribution de la diversité morphologique suggère qu'*A. comosus* trouve son origine dans le Nord de l'Amazonie, sur le bouclier guyanais et dans l'Orénoque, où toutes les variétés botaniques sont rencontrées, à l'exception d'A. *comosus* var. *bracteatus*, forme résultant d'une introgression avec *A. macrodontes*, et originaire du Sud du continent comme ce dernier (Coppens d'Eeckenbrugge et al., 1997a ; Duval et al., 1997). Les analyses de l'ADN chloroplastique par PCR-RFLP de Duval et al. (2003) confirment cette vision et montrent une diversité particulièrement élevée, avec des relations entre formes sauvages, cultivées et intermédiaires, sur les Guyanes, et une diversité élevée des formes cultivées à gros fruit dans l'Ouest de l'Amazonie. Ces données mettent en évidence que la forme sauvage *A.comosus* var. *ananassoides* est à l'origine des formes cultivées tant pour le fruit (*A.comosus* var. *comosus*) que pour la fibre (*A comosus* var. *erectifolius*). Dans ce dernier cas, les données moléculaires indiquent clairement des domestications multiples. L'apport de la seconde forme sauvage, *A.comosus* var. *parguazensis*, semble avoir été négligeable, aucun de ses marqueurs spécifiques n'ayant été observé dans les formes cultivées.

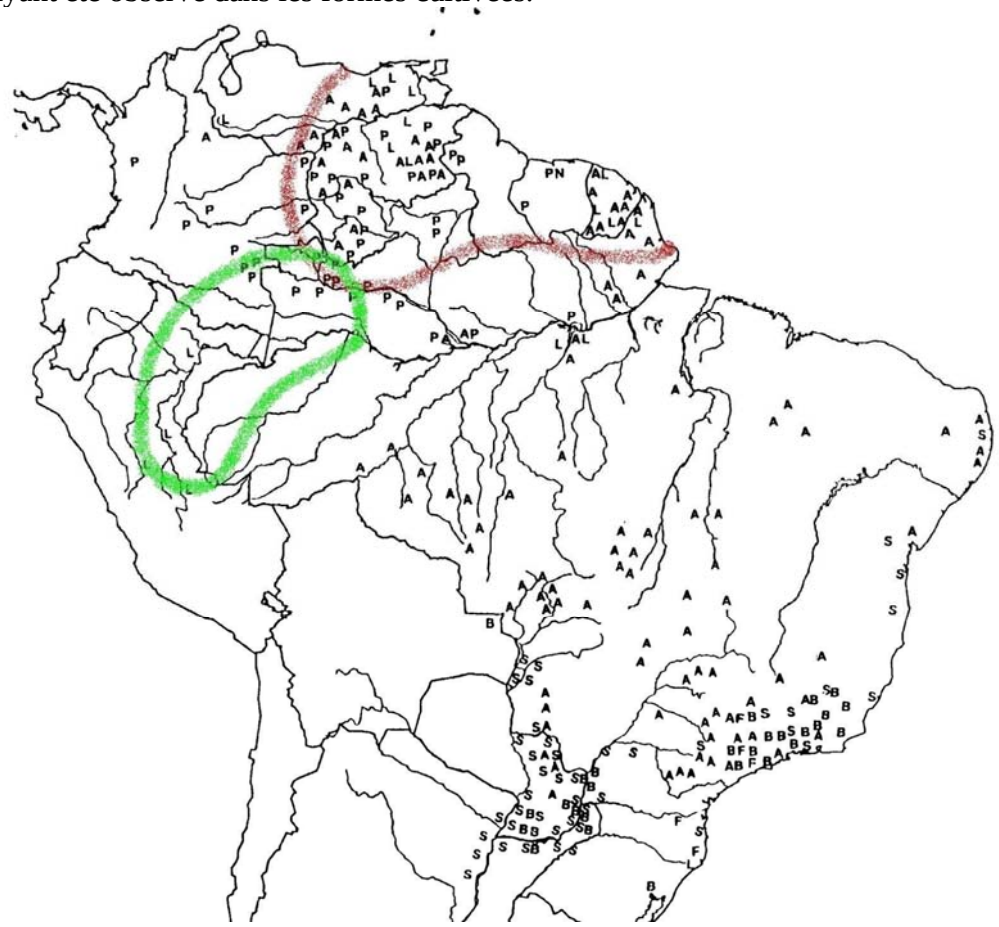

Figure 3. Distribution d'*A. macrodontes* (S) et des variétés *ananassoides* (A), *parguazensis* (P), *erectifolius* (L), et *bracteatus* (B) d'*A. comosus*. La ligne rouge indique le centre de diversité morphologique et génétique pour *A. comosus* (incluant var. *comosus* et des types intermédiaires entre les variétés *comosus* et *ananassoides*). Des formes partiellement épineuses y sont relativement fréquentes. La ligne verte indique une région de diversification secondaire de clones à gros fruit (typiquement var. *comosus*), où le caractère "piping" (feuille lisse ourlée) est relativement fréquent.

L'ensemble de ces données a été reprise récemment, avec des données de l'archéologie et de la glottochronologie (linguistique comparative historique), pour présenter une hypothèse générale sur la domestication des trois formes cultivées d'ananas (Figure 4 ; Coppens d'Eeckenbrugge et Duval, 2009 ; Coppens d'Eeckenbrugge et al., 2011). *A. comosus* var. *comosus* aurait été domestiqué au Nord-Est de l'Amazonie, dans la région des Guyanes, à partir de formes sauvages dont les fruits pulpeux croissent après l'anthèse. De telles formes intermédiaires, par les caractères des épines, du pédoncule et du fruit notamment, y existent toujours, suggérant de nombreux échanges liés au retour en conditions "sauvages" de formes cultivées primitives ou à la mise en culture de formes sauvages remarquables. Les formes cultivées auraient alors diffusé et/ou migré avec des populations d'horticulteurs, permettant l'établissement d'un centre secondaire de diversification dans l'Ouest de l'Amazonie, en l'absence de formes sauvages, absence qui expliquerait la disparition des caractères sauvages et la sélection de formes nouvelles issues de mutation (notamment la suppression totale des épines marginales liées au caractère "piping"). L'ananas y est encore de nos jours une plante d'énorme importance culturelle ("primary culturally defined keystone species"). De là, l'ananas se serait encore diversifié, pour s'adapter aux altitudes des contreforts andins et aux latitudes/altitudes mésoaméricaines, où il serait arrivé par les nombreux contacts avérés entre peuples andins et mésoaméricains, ou par diffusion progressive à travers l'Amérique Centrale. Les processus de domestication datent très vraisemblablement du début de l'Holocène, puisque l'ananas était cultivé sur les côtes du Pérou et de l'Equateur il y a plus de 3000 ans et au Mexique il y a plus de 2500 ans, selon les données archéologiques et glottochronologiques. Ce schéma général peut être replacé de manière cohérente dans le cadre général de la domestication ancienne des plantes amazoniennes les plus importantes et de leur diffusion préhistorique (Clement et al., 2010).

Le processus s'est déroulé différemment pour la domestication d'*A. como*sus var. *erectifolius*, ou *curagua*, ananas cultivé pour sa fibre. Très proche de sa forme parentale *A. comosus* var. *ananassoides*, il en diffère essentiellement par un port érigé, lié à la fibrosité de ses feuilles, un rejetonnage important et surtout l'absence d'épines, qui correspond à une mutation dominante et facilite l'extraction de la fibre. La relation forte entre la mutation et la domestication explique vraisemblablement que celle-ci se soit produite en différents endroits. En dehors de son aire d'origine, le Nord de l'Amazonie, la curagua ne s'est diffusée que vers les Antilles, accompagnant les migrations humaines. Sa diffusion vers d'autres contrées d'Amérique tropicale a probablement été freinée par l'exploitation d'autres Broméliacées terrestres à fibres, tant en Amérique Centrale et Mésoamérique qu'au Sud de l'Amazone, où elle entre en concurrence notamment avec *A. macrodontes*, plante épineuse il est vrai, mais permettant des productions économiques à partir de populations spontanées étendues et denses.

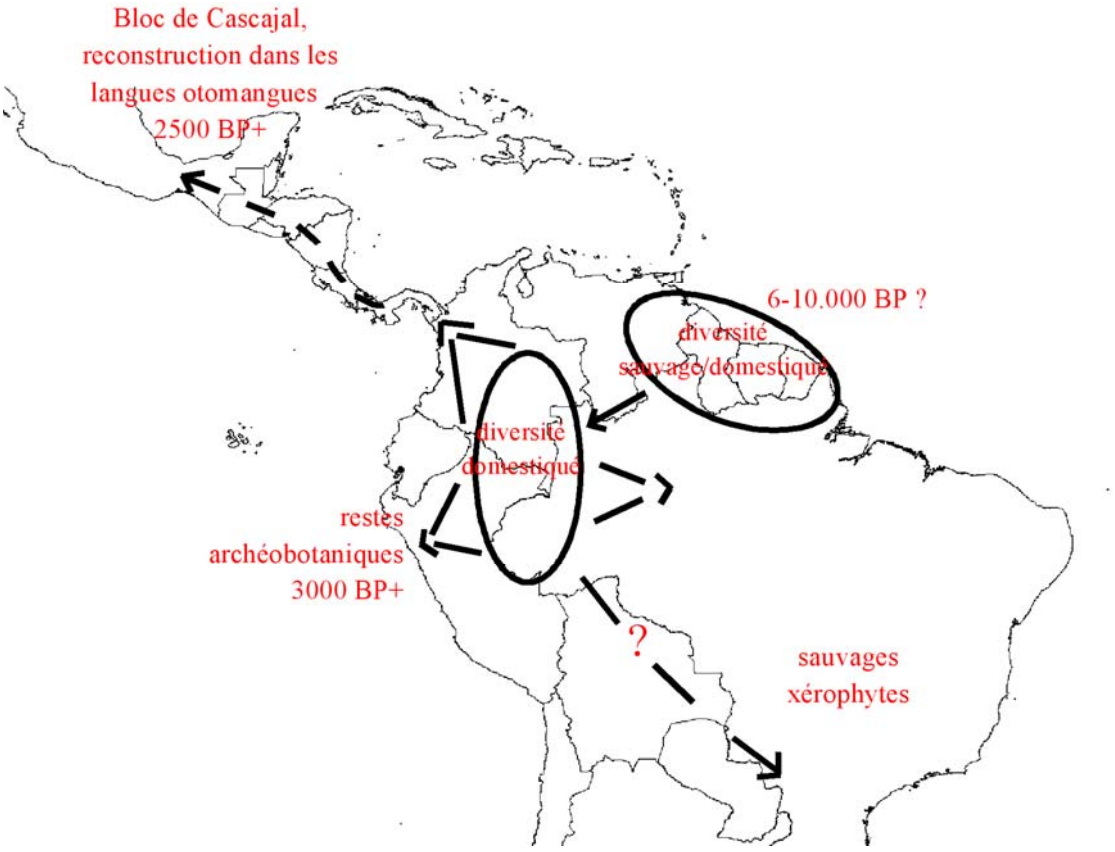

Figure 4. Géographie de la domestication et diffusion de l'ananas à gros fruit, à partir des données morphologiques, moléculaires, archéologiques et linguistiques.

Nos travaux et observations sur l'ananas permettent également de comprendre le processus de la domestication d'*A. comosus* var. *comosus* par la caractérisation du syndrome de domestication. L'allongement du cycle génératif par une réduction de la sensibilité à l'induction florale et le décalage entre rythme de croissance/culture et rythmes saisonniers (pluies, températures, photopériode), l'augmentation concomitante de la taille des feuilles et des organes de réserve (tige), le raccourcissement et renforcement du pédoncule (qui, avec la couronne du fruit, fait office de stolon chez les formes sauvages) élargissent l'adaptabilité de la culture, en la déconnectant de son climat d'origine et permettent la production d'un fruit beaucoup plus grand. La réduction de la fertilité et le renforcement de l'auto-incompatibilité permettent l'obtention de fruits aspermes et orientent une plus grande part des sucres vers la pulpe. Enfin, l'importance relative des ressources mises à la disposition de la formation d'un grand fruit, pouvant peser jusqu'à 13 kg et plus, la longueur des cycles végétatifs, rend la plante dépendante de conditions favorables (sol relativement riche et bien drainé) et d'une forme d'horticulture relativement intensive (jardins de case, pieds de souches dans les abattis jeunes) et limite sévèrement sa capacité de propagation spontanée, même dans son milieu d'origine. Alors que les ananas sauvages sont souvent des marqueurs de milieux pauvres (*campinas*, savanes-roches), l'ananas cultivé est tout au plus capable de végéter en sous-bois ou *cerrados* relativement ouverts.

Plus semblable aux formes sauvages, certaines curaguas n'en présentent pas moins des séquelles de millénaires de culture, surtout dans le rapport entre potentiels de reproductions végétative et sexuée. Ainsi, alors que certains clones sont très fertiles, d'autres présentent une propagation végétative tellement dominante que seules quelques tiges d'une touffe produisent un fruit, ou encore le nombre de fleurs est très réduit. La diversité des situations est vraisemblablement liée à la multiplicité des événements de domestication.

Plusieurs auteurs, dont certains parmi les plus influents (e.g. Zohary, 2004), ont attribué une importance extrême au clonage dans la domestication de plantes à propagation végétative dominante. L'idée était qu'il suffisait d'un cycle de propagation pour obtenir et exploiter un génotype d'élite apparaissant spontanément. L'étude du syndrome de domestication des ananas, et du processus évolutif nécessairement associé à son développement, est incompatible avec une telle domestication immédiate. Au contraire, il aura fallu beaucoup d'observation et de savoir-faire aux Amérindiens qui ont domestiqué ces plantes pour en manipuler la sexualité tout en favorisant la reproduction végétative. La lenteur de la germination et la fragilité des plantules d'ananas, jamais observée directement (même si Marie-France et moi avons parfois observé des situations suggérant fortement l'intervention effective de la sexualité dans des populations spontanées) posent nécessairement la question de l'intentionnalité dans le processus de domestication et de diversification des ananas cultivés pour le fruit.

2.2. Papayes

Avec les Caricaceae, nous visitons un groupe fruitier plus diversifié que le genre *Ananas*, même si la famille ne compte que six genres et 35 espèces. Seul un genre est africain, les autres sont américains. Les deux plus importants pour la fruticulture sont les genres *Carica* (monotypique ; papaye commune) et *Vasconcellea* (21 espèces ; papayes de montagne). Comme l'ananas, la papaye commune était déjà répandue dans toute l'Amérique tropicale lors du contact euro-américain et s'est propagée rapidement avec les grands voyages de la Renaissance. C'est un fruitier d'une grande importance sociale, de par sa large distribution pantropicale, mais aussi parce qu'il s'adapte aussi bien au jardin de case qu'à l'exploitation commerciale, quelle qu'en soit la taille. Sa production est à la fois élevée et constante, et il demande une main d'œuvre importante. Les papayes de montagne (*highland papayas* ou *mountain papayas*) tirent leur nom d'une distribution centrée sur les Andes, et plus particulièrement le Nord-Est de la Cordillère (de la Colombie au Nord du Pérou), particulièrement entre 750 et 2750 m (Scheldeman et al., 2007). A cause de cette distribution relativement restreinte et du fait qu'elles ne sont pas cultivées à très grande échelle, elles sont considérées comme des fruits mineurs, alors qu'elles peuvent être localement importantes (cas de la *papayuela*, *V. cundinamarcensis* en Colombie et des *babacos*, *V.* x *heilbornii* en Equateur) et qu'elles présentent un potentiel de développement important, pour le fruit frais ou la production de papaïne (Scheldeman et al., 2011). Enfin, le genre *Vasconcellea* constitue une source importante de caractères génétiques du plus grand intérêt pour l'amélioration de la papaye commune (Coppens d'Eeckenbrugge et al., 2013).

De par leurs fortes similarités de morphologie et d'utilisations, les genres *Carica* et *Vasconcellea* ont longtemps été traités comme un seul. Nos connaissances ont évolué récemment grâce à la confrontation des résultats de plusieurs groupes de recherche. Dès la fin des années 60, le Prof. Badillo (U. Centrale du Venezuela) a repris l'étude taxonomique, en collectant et observant de nombreux spécimens dans toute l'Amérique tropicale. Il a contribué à l'établissement d'une collection qui a permis d'étudier la reproduction des différents papayers (notamment la cytogénétique, le déterminisme sexuel et les compatibilités interspécifiques) au sein d'un programme d'amélioration du papayer commun (Profs. Jiménez et Horovitz). Le Prof. Badillo a été remarquablement attentif à intégrer les données expérimentales dans ses travaux de taxonomie. Dans les années 90, un groupe de recherche tropicale de l'Université de Gand a effectué des recherches ethnobotaniques dans un haut-lieu de diversité, la province de Loja au Sud de l'Equateur. Les collections établies à Loja ont pu être mises à profit par une équipe de généticiens de la même université, pour répondre aux questions posées par les observations des ethnobotanistes. Parallèlement, des équipes de recherches de Colombie, d'Equateur et du Costa Rica obtenaient un financement pour une étude des ressources génétiques des Caricaceae, dans un projet sous ma coordination. En favorisant les échanges de matériels et de méthode, ce projet a permis la confrontation des résultats et la rédaction de plusieurs synthèses importantes, fédérant les recherches menées dans les pays nord-andins et en Belgique et les reliant aux programmes d'amélioration menés par des chercheurs australiens.

Les Caricaceae sont des arbres ou arbustes laticifères, peu ramifiés, le plus souvent semi-ligneux, avec des feuilles souvent "palmo-lobulées", voire palmées. La plupart des espèces sont dioïques, et certaines présentent des cas d'andromonoécie. On trouve même un type sexuel complètement hermaphrodite (fleurs fonctionnellement bisexuées) chez les cultivars modernes de papaye commune. La différenciation des genres *Carica* L. et *Vasconcellea* Saint Hil. a essentiellement été basée sur le fait que l'ovaire est uniloculaire pour le premier et pentaloculaire pour le second (de Mello et Spruce, 1869). Cette différence, difficile à établir, a rapidement été mise en doute et les deux genres aussitôt réduits à deux sous-sections de *Carica* (Bentham et Hooker, 1867). Cette classification eut un impact important sur l'amélioration génétique du papayer commun, auquel on attribua longtemps une origine sud-américaine puisque c'est là que le genre *Carica sensu* Bentham & Hooker comptait le plus grand nombre d'espèces. Aussi, les papayes de montagne étant considérées comme rustiques ou primitives, c'est là que l'on chercha d'abord des résistances génétiques aux graves maladies du papayer commun, afin de les y introduire par hybridation. Badillo, observant à la fois les fréquentes hybridations entre papayers de montagne, tant spontanées qu'artificielles, et les difficultés qu'avaient ses collègues généticiens à les hybrider avec le papayer commun, proposa la réhabilitation du genre *Vasconcellea* en 1993, ce qu'il fit formellement en 2000, dès qu'il fut conforté par les résultats de l'étude de phylogénie moléculaire d'Aradhya et al. (1999). Celle-ci, basée sur des marqueurs PCR-RFLP de l'ADN chloroplastique, a depuis été confirmée par plusieurs études moléculaires (AFLP, PCR-RFLP, microsatellites et séquences) de l'équipe gantoise (Van Droogenbroeck et al., 2002 ; Kyndt et al. 2005b) et de mes étudiants (Restrepo et al., 2004b ; Ocampo et al., 2006). Cette situation, nouvelle lors du démarrage de nos projets en 1998, nous a conduits à traiter séparément les deux genres.

2.2.1. Papaye commune

Figure 5. Papayer sauvage (femelle) sur la côte Pacifique du Costa Rica (gauche) et papayer féral (hermaphrodite) en forêt camerounaise (droite).

Pour la papaye commune, la tâche était grandement simplifiée, puisqu'il nous fallait revenir aux rapports mentionnant l'existence de papayers sauvages. Selon Manshardt et Zee (1994), leur distribution suivait le versant Atlantique des territoires Mayas, depuis la péninsule du Yucatán au Petén (Guatemala). Nos prospections au Costa Rica nous ont conduits à l'élargir considérablement, puisque nous avons observé des plantes comparables aux brèves descriptions de Manshardt et Zee (fruits de la taille d'une balle de golf, remplis de graines) dans les forêts de la côte Pacifique du pays (Figure 5), tandis que nous avons trouvé des papayers spontanés, dont les caractères morphologiques montraient une évidente introgression avec des papayers cultivés en jardin de case sur les deux côtes, ce qui a été confirmée par la caractérisation morphologique détaillée. La taille du fruit étant rendue variable suite aux hybridations, la couleur jaune de la pulpe, et surtout sa charge en latex, étaient les meilleurs indicateurs de l'origine hybride des plants spontanés. Par ailleurs, alors que la diversité morphologique est élevée, la diversité enzymatique est très limitée, et son analyse ne permet pas différencier les types sauvages et cultivés (Coppens d'Eeckenbrugge et al., 2007). Ces résultats ont été largement confirmés par une récente étude basée sur des marqueurs microsatellites (Brown et al.,

2011). Selon nos observations, la distribution du papayer sauvage s'étend au moins jusqu'à l'Ouest du Panama. En revanche, les populations spontanées observées au Venezuela et en Colombie semblent correspondre à une régression de papayers cultivés vers l'état sauvage (plantes férales). Elles paraissent peu différentes des populations forestières spontanées, à petits fruits, que j'ai pu observer au Cameroun (Figure 5), sauf que ces dernières comprenaient des individus hermaphrodites, indiquant clairement qu'elles descendaient de cultivars modernes, d'introduction beaucoup plus récente.

L'effet le plus flagrant de la domestication de la papaye est l'augmentation considérable de la taille du fruit, passé de quelques dizaines de grammes à plusieurs kilogrammes chez la plupart des cultivars traditionnels. Corrélativement, le mésocarpe est passé de quelques millimètres à plusieurs centimètres. La pulpe a pris un ton orangé, tandis que le goût en a été amélioré par la réduction du contenu de latex et l'augmentation de sa teneur en sucre, permettant ainsi sa consommation en frais. Il est à noter que la taille du fruit ne régresse pas totalement dans les formes férales, qui gardent un fruit d'au moins 100g, dont les formes et la structure restent proches de celles des fruits cultivés. Les papayes cultivées ayant démontré une certaine capacité à revenir à l'état spontané, et à s'y maintenir, il est vraisemblable que la domestication n'en soit pas achevée. Pourtant, leur semence présente un syndrome de domestication assez clair, avec une augmentation en taille (33%) et une suppression de la dormance, alors que les papayes sauvages, en bonnes espèces pionnières, montrent une dormance durable des semences, lesquelles demandent une forte exposition à la lumière et sont sensibles aux alternances de température pour leur levée (Paz et Vázquez-Yanes, 1998).

Il est généralement admis que la sélection artificielle a favorisé les cultivars présentant le type sexuel hermaphrodite, qui dépendrait de l'homme pour son maintien (Horovitz et al., 1953). Cette assertion est contredite par mon observation de populations comprenant des plants hermaphrodites à petits fruits dans certaines forêts au Cameroun. Le lien entre domestication et hermaphroditisme a d'ailleurs été fortement mis en cause par l'étude de Yu et al. (2008) qui estiment que le chromosome Yh de ce type sexuel aurait divergé du chromosome Y des types mâles il y a plus de 73.000 ans, donc bien avant les débuts de l'agriculture.

2.2.2. Papayes de montagne

La figure 6 présente les trois papayes de montagne les plus cultivées : le babaco du Sud de la Colombie et de l'Equateur, et les deux papayuelas andines.

Figure 6. Fruits de babaco (*V.* x *heilbornii*) et de papayuelas (*V. cundinamarcensis* et *V. goudotiana*).

V. cundinamarcensis se rencontre du Vénézuéla au Chili ; elle est particulièrement commune en Equateur et en Colombie. Elle est souvent assimilée à un fruitier de jardin de case et son importance économique est ainsi sous-estimée. Or, même pour une espèce mineure, les marchés urbains de Colombie, notamment Bogotá, lui assurent un débouché relativement important. Par ailleurs, introduite au Chili, elle y est cultivée pour la conserve, et son fruit exporté. L'espèce se présente très différemment en Colombie et en Equateur. Dans le premier pays, la plante est fortement pubescente, le fruit moyen, vert à jaune, de la taille d'une pomme, et modérément côtelé ; les populations sauvages semblent rares et ne sont pratiquement pas documentées. Dans le second pays, la pubescence caractéristique de l'espèce est considérablement réduite, disparaissant parfois presque entièrement ; le fruit est jaune ou fortement anthocyané, plus petit et fortement côtelé ; la plante, tolérée, pousse de manière spontanée dans les milieux perturbés. Faute de connaître les populations sauvages, il est difficile d'apprécier la progression de la domestication chez *V. cundinamarcensis*. L'espèce s'est naturalisée dans des zones d'altitude du Sri Lanka, de l'Inde, de Nouvelle Zélande, de Puerto Rico (Morton, 1987) et de Zambie (données recueillies sur herbier à Kew), ce qui montre que certaines populations cultivées au moins n'ont pas perdu leur capacité de propagation naturelle. Si certaines populations ont été réellement domestiquées, cela n'a pu se produire que dans le Nord des Andes (Colombie, éventuellement Venezuela), comme en atteste l'existence de fruits plus gros et bien plus homogènes sur les marchés colombiens. Mais ce critère n'est pas fiable. La seule population que nous ayons pu observer sous forêt secondaire en Colombie donnait des fruits de forme moins régulière mais de taille comparable.

L'autre *papayuela*, *V. goudotiana*, est cultivée en Colombie, où nous avons pu en observer deux populations spontanées. Celles-ci se trouvaient en situation de piedmont (500 et 1000 m d'altitude), alors que la culture se donne à plus grande altitude (2000 m et au-delà) et la taille des fruits, légèrement plus petite, pouvait s'expliquer aussi bien par une différence de milieu que par une différence entre populations sauvages et cultivées.

Enfin, une étude de la diversité enzymatique, menée par un de mes étudiants (Jiménez et al., en préparation), a montré une structuration très forte en fonction de la géographie, les espèces colombiennes se différenciant des équatoriennes. Dans notre échantillon, *V. cundinamarcensis* était la seule espèce commune aux deux pays. Ses représentants se différenciaient fortement en fonction de leur origine, montrant de plus fortes affinités géographiques que conspécifiques, révélant ainsi de forts niveaux d'introgression entre espèces sympatriques. Les différences morphologiques observées entre les deux pays sont vraisemblablement liées à de telles introgressions. Ainsi, la moindre pubescence ainsi que la petite taille et le caractère fortement côtelé des fruits équatoriens pourraient provenir d'hybridations répétées avec *V. stipulata*, espèce spontanée et de jardin de case présente au Sud de l'Equateur.

La troisième papaye de montagne cultivée commercialement, *V.* x *heilbornii*, a d'ailleurs été décrite comme un hybride entre *V. cundinamarcensis* et *V. stipulata*. Badillo (1993) en a décrit trois formes, dont la plus connue est le babaco, qui donne un grand fruit en forme d'obus. D'autres formes, donnant des *higachos* ou *baby-babacos*, plus parfumés et moins grands, prennent une importance croissante car ils sont mieux adaptés aux marchés urbains que de trop gros fruits. Réputé stérile, le babaco se propage uniquement par bouturage. A première vue, sa domestication semble donc liée à la propagation exclusivement végétative d'un hybride exceptionnel. Les études des diversités morphologiques et moléculaires nous ont amenés à percevoir un processus d'évolution sous domestication beaucoup plus complexe.

Une première étude sur du germoplasme sud-équatorien (Scheldeman, 2002) avait déjà montré une grande diversité morphologique, particulièrement chez *V.* x *heilbornii*, brouillant les limites avec *V. stipulata* et suggérant que la sexualité jouait encore un rôle sporadique mais important dans la reproduction du matériel cultivé. Différentes études par marqueurs, AFLP et microsatellites, ont confirmé une forte diversité génétique chez les formes hybrides, avec une variation AFLP considérable même au sein du babaco, les matériels cultivés se plaçant dans une position intermédiaire entre les parents putatifs, avec un groupe d'accessions plus proche de *V. stipulata* et un autre plus proche de *V. cundinamarcensis*, situation qui suggère un processus d'introgression bi-directionnel (Van Droogenbroeck *et al.* 2002, Kyndt *et al.*, 2005a, 2006).

Nous avons repris des études semblables en réunissant des matériels équatoriens et colombiens, et avons confirmé une diversité morphologique des baby-babacos surprenante pour des plantes propagées par voie clonale (Restrepo et al., 2004a). Même le babaco formait deux groupes morphologiques distincts, contredisant sa description comme cultivar dans la dernière classification. Nous avons pu observer une structuration géographique, les babacos et baby-babacos du Sud de l'Equateur apparaissant plus

proches de *V. stipulata*, espèce qui est précisément endémique de cette région. Cette structure géographique était confirmée par l'analyse de la diversité enzymatique mentionnée plus haut.

Une étude de l'ADN chloroplastique par PCR-RFLP (Restrepo et al., 2004b) a également révélé une grande diversité d'haplotypes au sein de chaque taxon, même pour le babaco, (20 haplotypes pour les deux espèces parentales et leurs hybrides), seul un haplotype apparaissant commun à deux taxons (*V. stipulata* et *V.* x *heilbornii* var. *chrysopetala*). Les haplotypes des hybrides divergent plus fortement de ceux de *V. cundinamarcensis* que de ceux de *V. stipulata*. Enfin, les haplotypes du babaco apparaissent très proches de celui d'une troisième espèce, *V. weberbaueri*.

La complexité de cette situation a conduit Van Droogenbroeck et al. (2006) à reprendre leurs analyses AFLP/PCR-RFLP sur un échantillon plus large, avec une attention particulière pour les fragments spécifiques des parents potentiels et des espèces les plus proches dans leur phylogénie du genre (*V. stipulata*, *V. cundinamarcensis*, *V. weberbaueri* et *V. parviflora*). L'analyse combinée des chlorotypes/mitotypes et des marqueurs AFLP spécifiques s'est avérée particulièrement informative (Tableau 2). La plupart des accessions de *V.* x *heilbornii*, y compris les babacos, présentent le même chlorotype que *V. weberbaueri*, et peu de marqueurs AFLP spécifiques de *V. stipulata*. Les autres présentent un chlorotype et un plus grand nombre de marqueurs AFLP spécifiques de *V. stipulata*. Un petit sous-groupe de ce dernier présente également de nombreux marqueurs AFLP spécifiques de *V. cundinamarcensis*. Le contraste est remarquable entre l'apport de cette espèce parentale supposée, dont la contribution apparaît comme sporadique et limitée au génome nucléaire et l'apport inattendu de *V. weberbaeuri*, semblant contribuer aux génomes cytoplasmiques et nucléaires, alors que c'est une espèce rare qui n'a pu jouer qu'un rôle très ancien et indirect dans la constitution des formes hybrides actuelles. Pour Van Droogenbroeck et al. (2006), ces résultats suggèrent l'existence d'un mécanisme menant à une perte disproportionnée des gènes spécifiques de *V. cundinamarcensis* dans les descendances des back-cross de *V.* x *heilbornii*.

Tableau 2. Distribution des marqueurs PCR-RFLP cytoplasmiques et des marqueurs AFLP spécifiques entre *V.* x *heilbornii* et les trois espèces impliquées dans son évolution (Van Droogenbroeck et al., 2006).

Taxon (nb d'accessions)	Chlorotype (ADNcp)	Mitotype (ADNmt)	Nb de marqueurs AFLP exclusifs		
			V. stipulata	*V. cundinamarcensis*	*V. weberbaueri*
V. stipulata (4)	S	H	24	0	0
V. cundinamarcensis (8)	C	C	0	47	0
V. weberbaueri (5)	H	H	0	0	21
V. parviflora	P	P	0	0	0
V. x *heilbornii* (10)	S	H	19 - 24	0 (7cas), 1, 4, 47	0 - 2
V. x *heilbornii* (20)	H	H	10 - 21	0 – 1, 6 (1 cas)	0 - 2
V. x *heilbornii* babaco (3)	H	H	8 or 12	0	2
V. x *heilbornii* (5)	H	H	10-21	46 - 47	0 - 1

Un tel mécanisme favorisant les gènes de *V. stipulata* avait déjà été suggéré par les études cytologiques de De Zerpa (1980). Utilisant des hybrides artificiels de *V. cundinamarcensis* et *V. stipulata*, cette chercheuse vénézuélienne avait observé un défaut d'homologie dans la méiose au niveau de la génération F1. La méiose ne se régularisait qu'au niveau de la génération BC2, phénotypiquement similaire à *V. stipulata*.

Néanmoins, dans une révision collective (Scheldeman et al., 2011), nous avons repris cette interprétation et j'ai proposé un modèle plus simple, "de terrain", pour expliquer le moindre apport de *V. cundinamarcensis*, dans un processus d'évolution sous domestication. Les premiers acteurs y sont deux espèces sympatriques du Sud de l'Equateur et du Nord du Pérou, *V. stipulata* et *V. weberbaueri*, qui forment un clade particulier de *Vasconcellea* avec une troisième, *V. parviflora*. L'actuelle diversité des génomes chloroplastiques suggère des introgressions très anciennes, à moins qu'une partie de cette diversité soit pré-existante à ce clade, ce qui expliquerait la diversité intra-spécifique observée. Les deux hypothèses ne sont pas exclusives dans un genre jeune qui manifeste tant de symptômes d'évolution réticulée. *V. cundinamarcensis* est probablement entrée en scène avec l'homme. En effet, bien qu'elle ne fasse pas partie du même clade que *V. stipulata* et que de faibles barrières interspécifiques existent déjà, son hybridation est favorisée par différents facteurs. D'abord l'espèce est très commune et plus largement adaptable que les espèces endémiques, ce qui augmente la fréquence potentielle des hybridations et peut affecter l'adaptation de leurs descendances. Le fruit des hybrides est significativement plus grand, de forme plus régulière que celui de *V. stipulata*. Il peut être produit de manière parthénocarpique, et la propagation par bouturage permet l'exploitation des seuls plants femelles. Dans ces conditions, la rareté de la pollinisation et les barrières interspécifiques rendent les plants stériles, et la rareté des semences facilite grandement le traitement et la consommation des fruits. La seule source de pollen est constituée par d'éventuels plants mâles de *V. stipulata* et/ou *V. cundinamarcensis* aux alentours des parcelles cultivées. Les rares graines qui en résultent produisent un mélange de plants femelles et mâles. Les premiers peuvent être soumis à une sélection clonale drastique, tandis que les seconds, inutiles pour l'horticulteur, sont éliminés des parcelles de production. Un tel processus ressemble au schéma de diversification clonale du manioc par l'exploitation de la reproduction sexuée spontanée, suivie de sélection clonale (Elias et al., 2000, 2001), si ce n'est que la forme cultivée est d'origine hybride et que l'enrichissement de ce matériel dépend de rétrocroisements avec les formes parentales, tolérées aux abords des cultures. En effet, le système est contraint par la combinaison de la dioécie et de la parthénocarpie. C'est lui aussi qui explique le déséquilibre dans la contribution des formes parentales, la plus commune apportant moins que la forme endémique. Au niveau de la parcelle, la culture étant essentiellement constituée de formes femelles de *V.* x *heilbornii*, les recombinaisons entre hybrides sont presque impossibles. Les rétro-croisements avec les plants femelles des espèces parentales ne le sont guère d'avantage. En effet, il ne semble pas logique d'aller chercher la semence d'une forme fruitière dans les fruits d'une autre forme, même apparentée. Quand bien même le processus serait connu du cultivateur, comment trouverait-il ces rares semences hybrides parmi toutes celles qui ne le sont pas ? La seule possibilité de reproduction sexuée implique donc des plants mâles des espèces parentales.

Elle favorise nécessairement *V. stipulata*, puisque le croisement de retour sur cette espèce est cinq fois plus fertile que sur *V. cundinamarcensis* (Horovitz et Jiménez, 1967). Dans les rétrocroisements suivants, la sélection en faveur de génotypes présentant une meilleure homologie à la méiose renforcera encore l'avantage des éléments de génome de *V. stipulata*. Enfin, la sélection artificielle élimine vraisemblablement les phénotypes divergents de l'idéotype du babaco, ce qui explique que, parmi les caractères de *V. cundinamarcensis*, ne se maintiennent que des caractères végétatifs ou floraux sans importance pour les paysans (faiblesse des stipules, couleurs des pièces florales).

Si, dans ce système, l'apport génétique de *V. cundinamarcensis* est fortement limité, et à plusieurs niveaux, l'espèce n'en a pas moins été essentielle, non seulement à l'origine du processus, mais aussi probablement dans son maintien. En effet, elle reste propagée par la semence, et sa culture a pu maintenir la pratique d'utiliser même les rares semences de babaco disponibles. Quant au processus lui-même, il fournit encore un exemple de la "fausse simplicité" de l'exploitation de la reproduction végétative dans la domestication des plantes.

Rappelons encore que les processus d'introgressions entre plantes spontanées sont vraisemblablement beaucoup moins contraints, comme le montre la structuration des diversités morphologique et enzymatique chez *V. cundinamarcensis*, où la logique géographique l'emporte largement sur les barrières interspécifiques, ce qui confirme a contrario que c'est bien la gestion humaine qui crée et maintient des formes hybrides déséquilibrées dans un système dynamique.

2.3. Passiflores

Avec les passiflores, nous franchissons encore un degré dans la complexité et la diversité. En effet, le genre *Passiflora* compte entre 500 et 600 espèces, américaines dans leur grande majorité. J'en ai inventorié plus de 80 dont le fruit est consommé, au moins occasionnellement (Coppens d'Eeckenbrugge, 2003). Une douzaine d'espèces semblent domestiquées. Et parmi leurs si nombreuses congénères sauvages, beaucoup présentent un potentiel économique équivalent. La taxonomie est donc essentielle à l'approche de ces plantes fruitières. Jusque récemment, c'est l'œuvre de Killip (1938, 1960), classant le genre en 22 sous-genres, qui faisait autorité, ne subissant que des modifications relativement mineures, comme l'addition d'un sous-genre par Escobar (1989). Une nouvelle classification a été proposée par Feuillet et McDougal (2004), réduisant le premier niveau à quatre sous-genres, eux-mêmes divisés en supersections, sections et séries. Les trois sous-genres les plus nombreux sont clairement supportés par les études moléculaires, notamment celle que nous avons conduite avec J. Ocampo (Ocampo et al., en préparation). Ils correspondent à des divisions morphologiques et cytogénétiques fortes. Le sous-genre *Astrophea* compte une majorité d'espèces arborescentes à 2n=24 chromosomes, le sous-genre *Decaloba* (2n=12) est constitué de lianes herbacées à petites fleurs et petits fruits, pollinisées surtout par de petites abeilles et guêpes, et le sous-genre *Passiflora* (2n=18) se caractérise par des espèces herbacées à ligneuses, donnant de grandes fleurs, pollinisées par de grosses guêpes ou des colibris, et donnant de grands

fruits. Le quatrième sous-genre, *Deidamioides*, est plus difficile à caractériser morphologiquement dans son ensemble ; il a d'ailleurs été malmené par les études moléculaires, dispersant ses treize espèces actuelles dans les reconstructions phylogénétiques. Aux niveaux inférieurs, celles-ci ne supportent que quelques supersections (Yockteng et Nadot, 2004). Aux défauts de la classification elle-même, liés à une approche morphologique partiellement intuitive et à une multiplicité de niveaux inférieurs (contrecarrant la simplification au niveau des sous-genres), s'ajoutent les problèmes liés à l'interprétation des données moléculaires, singulièrement compliquée par un haut degré de réticulation dans l'évolution et la complexité de la transmission des différents génomes dans le genre. Les hybridations interspécifiques sont relativement communes et la transmission des chloroplastes est souvent paternelle ou biparentale. Celle des mitochondries est inconnue, mais nos résultats divergent très fortement de ceux attendus sur base d'une transmission maternelle. Enfin, une difficulté supplémentaire vient de ce que la nouvelle classification n'a pas été achevée, et de très nombreuses espèces doivent encore y être incluses.

Les aspects systématiques (diversité morphologique, diversité génétique, distribution et adaptation) ont eu une grande importance dans nos travaux sur les passiflores, à cause de la nécessité de dresser un inventaire des objets d'étude et de débrouiller l'écheveau des relations entre espèces et taxons infraspécifiques, même pour les plus courants. J'ai monté et coordonné trois projets successifs, l'un au niveau régional (réseau andin de ressources phytogénétiques, REDARFIT), les deux autres en partenariat avec des institutions colombiennes (et le financement de Colciencias puis Cenicafé), qui nous ont permis de collecter un grand nombre d'accessions. Mes étudiants et moi-même avons notamment réuni la collection la plus diverse jamais rassemblée, et avons pu l'installer à deux altitudes différentes. Les très lourds travaux de caractérisation morphologiques (jusqu'à plus de 150 descripteurs) ont été doublés d'études palynologiques, cytologiques et moléculaires (AFLP, PCR-RFLP), qui ont notamment fait l'objet de la thèse de John Ocampo. Nous avons repris récemment des études semblables en Guyane, avec un étudiant en mastère, Maxime Rome. La valorisation de cet ensemble très riche de données est encore en cours. Ils ne peuvent être présentés ici en détail, d'autant plus que cette présentation est restreinte à la problématique de la domestication des espèces fruitières. Nous nous contenterons donc de présenter la situation des principales espèces de passiflores cultivées, et les questions qui se posent en termes de domestication.

Les nombreuses espèces dont le fruit est consommé se répartissent équitablement entre les sous-genres *Decaloba* et *Passiflora* (Coppens d'Eeckenbrugge, 2003). Mais les fruits étant généralement petits chez le premier (rarement plus de 1,5 cm de diamètre), c'est logiquement dans le sous-genre *Passiflora* que l'on trouve les espèces d'intérêt horticole. Si leur relation avec l'homme est ancienne (Patiño, 2002), leur développement commercial est récent. Le développement du maracuja pourpre date de 1930. La description botanique du maracuja jaune, pourtant un cultigène, ne date que de 1932 et son développement à Hawaii attendra la fin des années 50. Seul son retour sur ses terres néotropicales lui permettra de "décoller" véritablement, dans les années 90. Les curubas, de la supersection *Tacsonia*, ne passeront du jardin de case à la culture commerciale qu'en 1957, peu après la grenadille douce (Yockteng et al., 2011).

Aujourd'hui, plus d'une quinzaine d'espèces sont cultivées, dont une douzaine à un niveau commercial (Tableau 3). Le maracuja est, de loin, la plus importante. Sa forme jaune, *P. edulis* f. *flavicarpa*, est cultivée dans la plupart des zones tropicales basses, particulièrement en Amérique du Sud. Le Brésil en est le premier producteur et consommateur, l'Equateur le principal pourvoyeur du marché international, la Colombie, en troisième position, pourvoyant un marché national relativement important. *P. edulis* f. *flavicarpa* est un cultigène, et son parent sauvage est inconnu. La forme pourpre, *P. edulis* f. *edulis*, est originaire du sud du continent, et d'ailleurs confinée à des climats plus frais, soit à des latitudes subtropicales, soit à des altitudes plus élevées, ce qui explique sa naturalisation récente dans le Nord des Andes et l'importance des pays d'Afrique de l'Est dans sa production actuelle. A la différence de la forme jaune, *P. edulis* f. *edulis* existe encore dans son habitat d'origine et s'est montrée capable de se renaturaliser hors de son aire naturelle. Les deux formes diffèrent non seulement dans leurs exigences climatiques, mais aussi dans leur biologie florale (moment de l'anthèse, auto-incompatibilité stricte chez la seule forme jaune) ; leur hybridation révèle une incompatibilité unilatérale. Malgré l'introgression artificielle de caractères "pourpres" dans la forme jaune, une caractérisation morphologique basée sur un grand nombre de caractères permet de les séparer aussi clairement que par des marqueurs AFLP ou par une étude PCR-RFLP de l'ADN chloroplastique ou mitochondrial (Ocampo et al., 2004 ; Ocampo et al., en préparation). Le statut conspécifique actuel des deux formes est douteux, tout comme une éventuelle contribution de la forme pourpre à l'origine du maracuja jaune.

P. incarnata, ou *maypop*, est tellement proche de *P. edulis* que les deux espèces ont longtemps été considérées comme synonymes. Les deux espèces forment le cœur de la section Incarnatae. *P. incarnata* est très commune dans certains états des Etats-Unis, s'y maintenant dans le sol pendant l'hiver tempéré pour en jaillir au mois de mai. Les écrits de voyageurs européens indiquent qu'elle était amplement cultivée par les Amérindiens lors de la conquête européenne, et il est très vraisemblable qu'elle était en voie de domestication. Malheureusement, le germoplasme cultivé s'est abîmé en même temps que les sociétés qui le reproduisaient et les cultivars actuels n'intéressent plus que l'horticulture ornementale.

La grenadille douce, *P. ligularis*, est cultivée commercialement dans le Nord des Andes, surtout en Colombie, où elle a visiblement fait l'objet d'une sélection efficace, ainsi que dans les régions d'altitude d'Amérique Centrale, où le fruit présente une forme oblongue différente de la forme "en oignon" connue dans les Andes. Je n'ai jamais pu en observer à l'état sauvage, dans les Andes tout au moins. Il s'agit vraisemblablement d'un cultigène. Curieusement, *P. tiliifolia*, une espèce sauvage très proche, tant par les principales caractéristiques végétatives que par celles du fruit, peut souvent être observée dans les mêmes zones où l'on cultive *P. ligularis* (elle est même venue s'installer spontanément dans notre collection de *P. ligularis*). Elle est parfois mise en culture, par transplantation de jeunes individus sauvages, mais rien n'indique qu'elle puisse être à l'origine de *P. ligularis*. Une première étude AFLP a indiqué que les deux espèces sont génétiquement proches, mais restent distinctes (Ocampo et al., 2004). La série des Tiliifoliae compte

encore bien d'autres espèces morphologiquement très proches de *P. tiliifolia* et *P. ligularis*, notamment *P. triloba* et *P. palenquensis*, cultivées dans des zones forestières retirées, en basse altitude.

Tableau 3. Principales espèces commerciales de fruits de la passion. D : domestiquée, ND : non domestiquée ; DI : domestication intermédiaire (caractères de domestication mais dépendance incomplète à la culture).

Espèce	Populations spontanées	Populations cultivées	Adaptation à la culture	Statut
P. edulis f. *flavicarpa*	inconnues	pantropical	semences non dormantes	D
P. edulis f. *edulis*	Sud Brésil, Nord Argentine, Paraguay ; féral dans les Andes tropicales	pantropical et subtropical	semences non dormantes	ND (DI)
P. ligularis	inconnues	du Mexique aux Andes tropicales	semences non dormantes	D
P. maliformis	Colombie ?	Colombie (culture), Antilles (jardins de case)	?	Indét.
P.quadrangularis	inconnues	Amérique tropicale	?	D
P. alata	Centre du Brésil	Sud du Brésil	germination erratique	ND
P. laurifolia	Guyanes, féral aux Antilles ?	Antilles	?	Indét.
P. nitida	?	Amérique tropicale	Végétation excessive	D
P. popenovii	inconnues	Sud de la Colombie et de l'Equateur	germination erratique, difficile ; végétation excessive	D
P. tripartita var. *mollissima*	Sud Equateur (autres variétés botaniques) ; Colombie ?	Andes tropicales	semences non dormantes	D
P. tarminiana	inconnues ; espèce invasive dans certaines îles	Andes tropicales	semences non dormantes	D

P. maliformis, appelée *granadilla de piedra* ou *granadilla de hueso*, ou encore coque-en-fer, en référence à la dureté de son péricarpe, a été également classée parmi les Tiliifoliae. Ni l'analyse morphologique détaillée, ni l'étude par marqueurs AFLP ne permettent de soutenir cette classification (Ocampo et al., 2004). Cette espèce très polymorphe ne semble pas complètement domestiquée puisque nous l'avons observée à l'état spontané. Trois espèces très proches, *P. platyloba*, *P. serrulata* et *P. multiformis*, plus rarement cultivées, ne s'en distinguent que par des feuilles trilobées. La taille légèrement plus faible de leurs fruits est probablement liée à un niveau de sélection négligeable.

Figure 7. Fruits de la passion d'importance économique : Incarnatae : *P. edulis* f. *flavicarpa* et *P. edulis* f. *edulis* ; Tiliifoliae : *P. ligularis* & *P. maliformis* ; Quadrangulares : *P. quadrangularis* & *P. alata* ; Laurifoliae : *P. laurifolia* & *P. popenovii* ; Tacsonia : *P. tripartita* var. *mollissima* & *P. tarminiana*.

Dans la série Quadrangulares, la barbadine, *P. quadrangularis*, donne un fruit géant (plus de 20 cm), cultivé dans toute l'Amérique tropicale. Son origine est inconnue. Il s'agit encore d'un cultigène. Fait remarquable, la culture impose une pollinisation manuelle. Le maracuja doux, *P. alata*, une espèce très proche, commune dans certaines régions amazoniennes et dans les forêts-galeries du plateau central brésilien, parfois cultivée en jardin de case, a récemment été mise en culture commerciale au Sud du Brésil. L'opération, très organisée et réussie, comprenait une sélection visant à assurer une

grande homogénéité dans la forme et la taille des fruits (Kavati et al., 1998). Curieusement, la semence semble poser autant ou d'avantage un problème de perte rapide de viabilité que de dormance.

La série des Laurifoliae comprend de nombreuses espèces très proches. Comme groupe, il est facile à identifier par une série de caractères morphologiques récurrents : feuilles "de laurier", une paire de nectaires aplatis sur le pétiole, fleurs souvent en pseudo-grappes, fruits relativement grands, oranges, à mésocarpe épais et spongieux, arilles très succulents, dans les deux sens du terme. Individuellement, des espèces si proches sont très difficiles à identifier et à différencier. L'espèce la plus souvent mentionnée est, logiquement, *P. laurifolia* ; sa distribution couvrirait les Antilles et toute la partie tropicale de l'Amérique du Sud, et elle y serait souvent cultivée. Pourtant, je ne l'ai jamais observée en Amétique du Sud hors de Guyane (aucune des équipes nationales du premier projet des pays andins n'a pu l'identifier), et elle ne semble cultivée qu'aux Antilles. La description du type botanique est trop imprécise, et même l'origine géographique, entre Antilles et Surinam, en est incertaine. L'espèce guyanaise généralement identifiée comme *P. laurifolia* est très commune mais sauvage. La forme cultivée aux Antilles semble différente, mais ces différences morphologiques pourraient être liées à un processus de domestication. La divergence entre les deux formes devra donc être vérifiée au moyen de marqueurs génétiques.

Alors que *P. lauriolia* ne semble exister qu'à l'état sauvage sur le continent, l'espèce cultivée en Guyane, comme ailleurs en Amazonie et dans le Chocó colombien, est *P. nitida*, qui semble être domestiquée. On peut l'observer à côté de Laurifoliae sauvages poussant aux abords des abattis. La passiflore sauvage montre alors clairement une plus grande capacité à envahir la parcelle cultivée que la passiflore cultivée à s'en échapper.

D'autres Laurifoliae sont cultivées ailleurs en Amazonie. En fait, une étude comparée serait nécessaire pour vérifier qu'il s'agit bien d'espèces différentes. Quelques espèces sont également cultivées à des altitudes moyennes. La plus remarquable est *P. popenovii*, qui donne un fruit rare et très recherché en Colombie et en Equateur. La reproduction de la plante est très difficile, la semence montrant un phénomène de dormance complexe. Certains génotypes ne sont maintenus que par bouturage ou marcottage. La culture est limitée à deux aires relativement bien délimitées et distantes, au Sud de la Colombie et au Sud de l'Equateur. Pour quelque raison difficile à cerner (notamment faute de pouvoir propager la plante pour des essais), nous sommes là devant un cas d'endémisme de plante cultivée. L'espèce est inconnue à l'état sauvage.

Nos études guyanaises, initiées par une recherche de Mastère (Maxime Rome) visent à caractériser les Laurifoliae présentes en Guyane Française, tant à l'état sauvage que cultivé, par une analyse morphologique et génétique fine. En même temps une caractérisation écoclimatique des espèces observées vise à cerner comment des espèces si proches dans leur morphologie et, apparemment, dans leur habitat (criques, bas-fonds fréquemment inondés), peuvent coexister. A terme, nous voudrions comprendre pourquoi dans un groupe homogène, où tous les fruits sont semblables en termes de qualité et de consommation, certaines espèces se prêtent mieux à la culture que d'autres, et comment

peut s'enclencher le processus de domestication. Nos premiers résultats valident les espèces décrites, sauf *P. gabrielliana* qui devra probablement être mise en synonymie. Une comparaison avec la forme cultivée du même nom aux Antilles devrait permettre de savoir dans quel sens modifier la classification pour la clarifier. L'étude de la distribution des différentes espèces sauvages validées montre qu'elles se différencient entre autres par des niches climatiques légèrement différentes, expliquant en même temps la diversité spécifique d'un taxon homogène dans un environnement qui paraissait lui-même relativement homogène. Sans surprise, l'espèce cultivée, *P. nitida*, semble prospérer dans l'ensemble des niches climatiques qui abritent ses cousines sauvages.

Enfin, parmi les passiflores les plus cultivées, figurent les curubas (Colombie) ou tacsos (pays de langue quechua), un groupe de passiflores très particulier, la supersection *Tacsonia*, dont la radiation récente est fortement liée au soulèvement andin (Ocampo et al., 2010). Le tube floral très long (7-13 cm) restreint l'accès normal au nectar, et donc la pollinisation, au seul colibri porte-épée, espèce qui a le bec le plus long. Le fruit en est allongé, avec un péricarpe mou. Chez les deux principales espèces cultivées, il est en outre jaune, d'où le nom anglais de *banana passion fruit*. Les deux fruits, reconnus et appréciés comme des variétés horticoles (*curuba de Castilla* et *curuba india*) par nombre de producteurs et de consommateurs, n'étaient pas reconnus par les botanistes. Les flores et monographies ne décrivaient que *P. mollissima* (en Colombie) ou *P. tripartita* var. *mollissima* (en Equateur). Paradoxalement, la forme non décrite a largement été diffusée par les collectionneurs de passiflores, sous le nom erroné de *P. mollissima*, et s'est naturalisée en de nombreuses régions tropicales d'altitude, devenant même invasive dans certains parcs nationaux aux Hawaï et en Nouvelle Zélande. Les deux formes s'hybridant aisément, il nous a fallu vérifier qu'il ne s'agissait pas de deux morphotypes divergents d'une même espèce. Nous avons donc entrepris la collecte et la caractérisation systématique des accessions collectées du Venezuela jusqu'au Pérou, établissant la diversité morphologique, enzymatique et moléculaire (AFLP) des deux formes et de leurs hybrides, artificiels ou spontanés (Villacis et al., 1998; Segura et al., 1998, 2000, 2002, 2003a, 2003b, 2005; Primot et al., 2005). Dès avant les derniers résultats, nous avons pu décrire la seconde forme comme une nouvelle espèce, *P. tarminiana* (Coppens d'Eeckenbrugge et al., 2001). Cette description a eu des conséquence pratiques pour l'amélioration (Primot et al., 2005), mais aussi pour la protection des parcs aux Hawaï et en Nouvelle Zélande, donnant un bel exemple de l'importance pratique de la taxonomie. En effet, l'identification correcte de l'envahisseur a permis de rechercher ses ravageurs spécifiques et de mettre en place un programme de lutte biologique efficace, alors que la même stratégie avait échoué avec les ravageurs de *P. tripartita* var. *mollissima*. Une autre source de satisfaction a été que la recherche des ravageurs spécifiques a été menée pour le compte des chercheurs néo-zélandais par Vicky Barney, l'étudiante colombienne qui m'a assisté dans la description de l'espèce. La capacité envahissante de *P. tarminiana* fournit également un exemple académique intéressant dans le cadre de notre recherche sur la domestication. En effet, malgré sa grande rusticité, *P. tarminiana* est un cultigène, et nous n'avons jamais pu l'observer en nature dans les Andes. L'introduction de la plante sans ses ravageurs n'explique que partiellement son caractère envahissant, puisque l'espèce est restée importante aux Hawaï malgré l'introduction des ravageurs. Les statuts de domestication ou de plante envahissante sont ici liés à l'écosystème où ils peuvent

s’exprimer, et le syndrome de domestication inclut vraisemblablement une perte/absence de caractères adaptatifs tant au niveau de la plante cultivée que de la communauté végétale où elle pourrait s’insérer. Aucun cas d’envahissement par une passiflore exotique n’a été rapporté aux Amériques, probablement parce que les communautés végétales ont évolué avec des passiflores natives. Pour compléter ce paragraphe sur *Tacsonia*, remarquons que *P. tripartita* var. *mollissima* est très rare en nature, et peut donc être considérée comme domestiquée. Les deux autres variétés botaniques de l’espèce sont endémiques du Sud de l’Equateur, où elles sont occasionnellement cultivées en jardins de case. D’autres espèces cultivées à petite échelle, comme *P. cumbalensis* ou *P. pinnatistipula*, sont encore très communes à l’état naturel.

Ce rapide examen des principales espèces de passiflores cultivées donne une image surprenante des phénomènes de domestication dans le groupe. Des taxons régulièrement cultivés à échelle commerciale (même locale) que nous avons listés, sept sont des cultigènes (*P. edulis* f. *flavicarpa*, *P. ligularis*, *P. quadrangularis*, *P. nitida*, *P. popenovii*, *P. tripartita* var. *mollissima* et *P. tarminiana*), et seulement trois (*P. edulis* f. *edulis*, *P. incarnata* et *P. maliformis*) ont maintenu des populations sauvages, ou régressent aisément à l’état sauvage dans leur milieu d’origine. La culture commerciale de *P. alata* est trop récente que pour apprécier son effet à long terme.

Il est difficile de trouver une explication dans les caractéristiques propres à chaque espèce. Les fruits des neufs cultigènes sont plus grands et leur pulpe plus abondante que ceux des trois autres, mais cette supériorité s’explique trop aisément par la sélection exercée de manière ininterrompue chez un cultigène. En outre, de nombreuses populations sauvages, notamment chez les Laurifoliae et Quadrangulares, soutiennent la comparaison quant à la taille du fruit et la quantité et qualité de sa pulpe. D’après notre expérience, la rapidité et la régularité de la germination sont fortement améliorées au moins chez *P. edulis* f. *flavicarpa*, *P. ligularis*, *P. tripartita* var. *mollissima* et *P. tarminiana*, mais elle l’est autant chez les populations cultivées de *P. edulis* f. *edulis*. Et la germination erratique si gênante pour la culture de *P. popenovii* pourrait même expliquer qu’au moins certains génotypes de cette espèce ne se reproduisent que végétativement, dans le cadre exclusif de leur culture. Un autre caractère important d’adaptation à la culture est une adaptation des lianes aux supports artificiels. Or, dans notre liste, les deux cultigènes de Laurifoliae, *P. popenovii* et *P. nitida*, se caractérisent par une croissance végétative profuse qui impose souvent de sacrifier la production de grands arbres du verger (e.g. avocatiers) pour leur fournir un support suffisamment solide. A l’inverse, les accessions sauvages de *P. alata* s’adaptent immédiatement aux supports artificiels. La régularité et la durée de la production déterminent également l’intérêt de la culture, mais certaines espèces sauvages occasionnellement cultivées soutiennent la comparaison avec les cultigènes, alors que, de nouveau, les Laurifoliae posent un problème particulier en concentrant leur production sur quelques semaines. Ce problème n’est compensé que par leur forte valeur sur le marché, même pendant le pic de production (que les producteurs attendent pour financer certains achats importants, comme les fournitures scolaires).

Faute de pouvoir l'expliquer par des caractéristiques intrinsèques des espèces, le nombre élevé de cultigènes surprend d'autant plus qu'il s'agit d'un groupe florissant, présent dans une grande diversité de milieux naturels ou perturbés, sur une niche très compétitive (les lianes constituant 25 à 44% des espèces ligneuses dans certaines forêts néotropicales ; Schnitzer et Brongers, 2002). Certaines espèces, hautement polymorphes (e.g. *P. foetida*, *P. suberosa*, *P. mixta*) occupent de larges aires de distribution, voire sont devenues pantropicales. Pour d'autres, manifestant un endémisme relativement étroit comme certaines Laurifoliae de Guyane, un polymorphisme comparable semble s'exprimer plutôt au niveau d'un groupe d'espèces étroitement apparentées, adaptées à des niches climatiques distinctes, bien que très proches. Dans ces conditions, on saisit difficilement comment certaines espèces ont évolué vers une dépendance si étroite vis-à-vis de l'homme, y perdant une bonne part de leur plasticité écologique.

La distribution des cultigènes au sein du sous-genre *Passiflora* n'est probablement pas anodine. Aucune de ces espèces très polymorphes et largement distribuées n'a donné de population domestiquée, même parmi celles qui sont parfois cultivées. Ainsi, *P. mixta* est parfois transplantée en jardin, voire cultivée très localement en Colombie ou au Venezuela. Certains petits producteurs commerciaux reconnaissent et favorisent les hybrides spontanés entre cette curuba sauvage et *P. tripartita* var. *mollissima* au sein de leurs parcelles, pour tenter d'y incorporer ses caractères de résistance, alors que d'autres les écartent dès la pépinière. Pourtant, jamais le processus n'a abouti à une adaptation de l'espèce à la culture, ni à l'introgression durable de caractères dans la forme cultivée. En revanche, il est possible que les cultigènes trouvent préférentiellement leur origine dans ces groupes d'espèces endémiques très proches dans leur morphologie et leurs adaptations, où les différentes espèces occupent des niches climatiques proches mais distinctes. Si l'habitat lié à la mise en culture permet à l'une d'elle d'évoluer en dehors de ses étroites contraintes climatiques originelles en relâchant le lien entre climat et habitat, elle peut perdre le lien avec sa petite population d'origine, par dérive génétique ou simplement par sa diffusion par l'homme. *P. nitida* pourrait avoir été domestiquée selon ce processus. Déracinée de sa niche originelle étroite, elle n'est plus compétitive que dans un jardin et se montre incapable de s'échapper vers la forêt immédiatement environnante où des formes proches occupent déjà la niche disponible. A l'appui de notre hypothèse de travail, remarquons que les deux maracujas (*P. edulis*) et le may-pop font vraisemblablement partie d'un tel complexe morphologique, bien que leurs milieux d'origine soient climatiquement très différents (respectivement tropical, subtropical et tempéré). La section Quadrangulares, d'où est issue la barbadine, compte également plusieurs espèces très proches. Si *P. alata* n'est pas une espèce endémique, l'exploration de l'Amazonie pourrait montrer l'existence d'espèces comme *P. trialata* et au moins une espèce non encore décrite, qui ne se distinguent que par des détails au niveau des stipules ou des nectaires. Dans la section des Tiliifoliae aussi, de nombreuses formes du Nord des Andes diffèrent entre elles par des détails similaires et semblent relativement endémiques, ce qui explique la difficulté pour identifier clairement les spécimens collectés. Enfin, de tels complexes existent tout aussi clairement chez les curubas. Les deux autres variétés botaniques de *P. tripartita* sont endémiques du Sud de l'Equateur. Autour de la curuba rouge, *P. cumbalensis*, et de la curuba antioqueña, *P. antioquiensis*, deux espèces dont la culture a été pratiquement abandonnée, existent encore ces

variations sur un même patron écomorphologique, produisant des endémismes favorisés par les reliefs andins.

Ce qui précède n'est qu'un début d'hypothèse de travail. Une partie de la clé se trouve dans la taxonomie, dont nous avons vu qu'elle est particulièrement complexe sur l'ensemble du genre, ou même dans le seul sous-genre *Passiflora*, à cause de la particularité de transmission des génomes et des évolutions réticulées. C'est pourquoi je m'intéresse de plus en plus à l'étude de ces complexes morphologiques clairement identifiables dans le sous-genre, préférant reprendre ainsi l'étude systématique du bas vers le haut.

2.4. Safoutier

Ma participation aux recherches sur le safoutier (*Dacryodes edulis*) a débuté dans le cadre d'un projet ANR intitulé IFORA (Ilots Forestiers Africains), lequel s'intéressait d'avantage aux espèces forestières sauvages et à la biodiversité qu'à la domestication. Néanmoins, il nous a fourni l'occasion d'étudier le genre en Afrique, et donc les relations de *D. edulis* avec ses parents sauvages, de collecter de nombreux matériels, tant sauvages ou subspontanés que cultivés, et de développer des marqueurs microsatellites pour l'étude des populations (Benoît et al., 2011). Nous avons également progressé dans une étude de la distribution du genre en Afrique et hors de l'Afrique.

A ce stade, nous n'avons que des résultats préliminaires, une partie seulement de l'échantillon ayant été exploitée, les analyses de la thèse de Gilbert Todou n'étant pas suffisamment avancées. Parmi les premiers résultats, nous avons observé une forte diversité des marqueurs microsatellites chez *D. edulis*. Elle se révèle plus importante que celle de *D. buettneri*, une espèce forestière. Cette diversité semble d'autant plus forte dans les populations camerounaises cultivées dans un but commercial. Les deux espèces étant allogames, l'explication se situe probablement dans la densité et la structure des populations et dans la différence des flux de gènes, plus importants dans les cultures commerciales qu'en forêt. Enfin, la différenciation génétique entre populations de safoutiers apparaît clairement entre Cameroun et Gabon (Todou et al., 2010).

3. Domestication, distribution et structuration sociale des ressources génétiques végétales - Travaux en cours et perspectives

Mes deux premières collaborations fortes avec des spécialistes des sciences humaines, notamment l'anthropologie sociale et la linguistique comparative historique, ont été riches en enseignements. Alors que nombre d'appels à projets soulignent l'importance d'approches équilibrées, prenant en compte à la fois les aspects biologiques et sociaux, et que nombre d'équipes cherchent à s'organiser dans le même esprit, je soutiendrais volontiers que les sciences sociales doivent avoir la prééminence dans la conception de telles recherches dès lors que l'objet de l'étude implique une "part de social" significative. Ainsi, si les ressources génétiques des plantes cultivées doivent être étudiées comme des objets sociaux, la première caractérisation doit se faire selon les méthodes en vigueur en sciences humaines, notamment celle développées en ethnoscience. Et il faudra toute la vigilance de l'anthropologue pour que la caractérisation ne vise pas à appliquer une grille d'analyse scientifique "occidentalisante" (étudier séparément les plantes et le contexte socioculturel) sur une réalité qui nous est étrangère et qui a sa logique propre (en considérant le contexte socioculturel) ; celle-ci doit être comprise, et non évaluée, pour caractériser plus finement les interactions entre les plantes cultivées et les sociétés humaines dans l'étude des processus de différenciation biologique et de domestication. Pour autant, cette priorisation dans l'objet de recherche n'impose aucunement que le biologiste renonce à son centre d'intérêt. Au contraire, il peut attendre, APRES l'ajout d'une dimension sociale à l'objet de ses recherches, une meilleure compréhension de ses propres résultats et une réorientation de ses questionnements.

Le respect d'une primauté des sciences humaines dans la conduite de recherches trouve évidemment ses limites au niveau du chercheur lui-même, qui doit garder par ailleurs une certaine autonomie dans le développement de son projet. Je me propose ainsi de maintenir **deux orientations** pour mes activités.

La première visera à documenter les processus d'évolution sous domestication dans leur diversité, en s'intéressant d'avantage aux espèces néotropicales pérennes, et plus particulièrement fruitières. Ce choix ne tient pas seulement à mon expérience sur ces espèces, mais aussi à ma conviction qu'il faut corriger le biais général des études (biologiques, ethnobotaniques, archéologiques) sur la domestication et le développement de l'agriculture aux Amériques. Celles-ci sont exagérément focalisées sur les plantes annuelles, et sur les céréales en particulier, ce qui ne me semble pas cohérent avec la somme des données accumulées sur la très grande diversité des interactions hommes-plantes en Amérique tropicale (voir section 3.1 ci-après). L'élargissement des études de la domestication à d'autres modèles biologiques, beaucoup plus diversifiés que les céréales, dans d'autres environnements culturels eux-mêmes très divers, apportera des éléments nouveaux sur les processus de domestication et les modalités de gestion du vivant (plantes, communautés, paysages) par les sociétés humaines à travers le monde (en considérant que les observations américaines peuvent éclairer les modes de gestion dans d'autres régions mégadiverses, en Afrique et en Asie). Pour étudier des contextes aussi riches, les espèces fruitières américaines présentent un modèle particulièrement

intéressant de par leur diversité même, en relation avec leur intégration dans des systèmes agroforestiers complexes, présumés plus résilients, et surtout de par notre méconnaissance de leur domestication. D'autres espèces pourront aussi être traitées, en fonction des collaborations possibles.

La seconde orientation tente d'élaborer des scénarios multidisciplinaires en considérant la spécificité non seulement des espèces du point de vue biologique, mais aussi celle des contextes historiques et culturels au sein desquels la domestication a pris place. Cette orientation sera développée via des collaborations avec mes collègues en sciences humaines. Décrire et analyser la structuration sociale des ressources génétiques et l'histoire des interactions passées entre plantes et sociétés (paléoethnobotanique notamment) en constitueront l'axe principal. Pour certains aspects (e.g. modèles de populations, sélection paysanne), de telles études peuvent être mieux fondées sur des cultures annuelles, dominantes dans de nombreux systèmes agricoles, comme c'est le cas pour le sorgho ou le maïs (Leclerc et Coppens d'Eeckenbrugge, 2012). Néanmoins, je souhaite développer une réflexion équivalente sur la diversité interspécifique et les communautés de plantes cultivées et/ou domestiquées, incluant donc la biodiversité représentée dans les espèces pérennes.

3.1. Domestication et relations hommes-plantes en Amérique tropicale

Si l'on veut mieux intégrer la biodiversité et particulièrement les plantes pérennes dans l'étude des relations hommes-plantes en Amérique tropicale, il nous faut remettre en question le modèle général de développement de l'agriculture qui a largement dominé les débats jusqu'à la fin du XXème siècle. Pour replacer les relations entre communautés humaines et végétales dans un contexte spatial et temporel plus large et plus ouvert, je propose ici une révision critique de l'état des connaissances générales sur le développement de l'agriculture et la domestication des plantes en Amérique tropicale.

3.1.1. XXème siècle : une vision étroite du développement au Nouveau Monde

Pendant longtemps, les phénomènes de domestication et le développement de l'agriculture aux Amériques ont été étudiés dans un contexte relativement étriqué. L'homme étant supposé un nouveau venu dans le système (arrivant en Amérique du Nord vers 10.000 BP), la préhistoire de l'Amérique tropicale, plus jeune encore, se limitait à un intervalle de quelques milliers d'années. Le développement de l'agriculture, lié à la sédentarisation et au développement technologique dans d'autres domaines (notamment la poterie), était fortement associé au développement des grandes civilisations qu'ont rencontrées les conquérants européens. Ce développement était perçu comme linéaire, ce qui s'exprime encore dans le découpage chronologique des époques culturelles (Paléo-Indien, Archaïque ou Pré-Céramique, Formatif, Classique, Post-Classique). Ce contexte général explique que les centres de domestication et de développement de l'agriculture définis par Vavilov montrent une relation géographique étroite avec ces civilisations de

Mésoamérique et des Andes qui ont laissé des traces monumentales durables et spectaculaires, tandis que d'immenses espaces semblaient vides d'agriculture et de civilisation. Une telle vision perdure et explique par exemple que Galindo et al. (2008) attribue la domestication de l'avocat aux Mokaya, vus comme civilisation-mère en Mésoamérique.

3.1.2. Biais culturel dans l'analyse

En même temps (et cela reste encore partiellement vrai), les théories sur la domestication des plantes et le développement des sociétés agricoles ont souffert de l'ethnocentrisme des chercheurs, dans leurs dimensions culturelle, spatiale et temporelle (voir par exemple le réquisitoire d'Anderson, 1997). C'est ainsi que les recherches les plus actives étaient menées dans le Croissant Fertile, berceau de l'agriculture occidentale, malgré l'apport considérable des plantes exotiques, notamment américaines, à l'agrobiodiversité mondiale. C'est aux très anciennes civilisations du Croissant Fertile qu'on a souvent attribué l'invention de l'agriculture. La forte relation présupposée entre agriculture et sédentarité, ou entre développement démographique et civilisationnel et sophistication des savoirs agricoles découle du même biais. C'est encore ainsi que l'on peut interpréter le côté passionnel des débats sur l'antériorité de l'agriculture et la domestication du blé, plante annuelle des mangeurs de pain, ou de l'horticulture et du figuier, plante pérenne (Kislev et al., 2006). C'est aussi le syndrome du Petit Chaperon Rouge qui peut expliquer la grande réticence à reconnaître des développements démographiques, culturels, agricoles, aquacoles et agro-forestiers de première importance dans l'"enfer vert" de la forêt tropicale humide, notamment en Amazonie ; à moins que ce ne soit lié au mythe de l' "Ecologically Noble Savage", voué à conserver une nature vierge (Meggers, 1971; Bailey et al., 1989 ; Headland et Bailey 1991; Alvard, 1993 ; Piperno, 2006 ; Hames, 2007). Même la focalisation sur le maïs et les hautes terres semi-arides en archéobotanique américaine n'est pas libre d'un biais culturel lié à certaines analogies avec le blé (Buckler et Stevens 2006 : "maize has been credited as the grain that civilized the New World").

3.1.3. Amérique du Sud : nouvelles dates, nouveaux modèles

L'accumulation des données et connaissances sur la domestication des plantes et le développement de l'agriculture a considérablement élargi le cadre de l'étude de ces processus, à la fois dans le temps et dans l'espace, en même temps qu'elles ont affaibli la distinction entre chasseurs-cueilleurs et agriculteurs. Les modèles de développement liant les débuts de l'agriculture, d'une part, et la sédentarisation des populations agricoles et/ou des développements technologiques particuliers (par exemple de la céramique), d'autre part, ne sont plus tenables (Roosevelt et al., 1991; Leclerc, 2012). En même temps, les débuts de l'agriculture ont été reculés à des dates de plus en plus anciennes. Les centres d'origine de l'agriculture et, partant, de domestication des plantes, se sont tellement multipliés depuis les travaux de Vavilov qu'ils en ont perdu du sens, ce qui avait déjà amené Harlan (1971) à corriger le modèle de diffusion de l'agriculture en distinguant des centres et des "non-centres", la Mésoamérique faisant partie des premiers et l'Amérique

du Sud des seconds. Pour l'Amazonie, par exemple, on peut au mieux analyser des tendances, comme le contraste entre un développement précoce accompagné de nombreux événements de domestication en périphérie et la concentration ultérieure de l'agrobiodiversité dans le centre du bassin (Clement et al., 2010).

Aux Amériques, la datation de plus en plus reculée des débuts de l'agriculture est liée à la démonstration de l'ancienneté du peuplement humain, laquelle a été difficilement imposée par les archéologues d'Amérique du Sud, contre le courant dominant au Nord, tenant d'une colonisation tardive (tradition Clovis). Ainsi, Dillehay et ses collaborateurs (1989) ont mis à jour les restes de 75 espèces végétales dans le site de Monte Verde, situé au Sud du Chili et daté de 12.000 à 13.000 BP. Ces restes correspondent aux parties utilisées ou consommées de ces plantes. Un quart d'entre elles sont exotiques, certaines ayant été importées de pas moins de 1000 km. A Monte Alegre, en Amazonie, les 58 restes de fruits consommés, de semences et de bois d'espèces amazoniennes ont permis des datations du site entre 11.200 et 10.000 BP, reculant la préhistoire des chasseurs-cueilleurs forestiers jusqu'à la fin du Pléistocène et démontrant l'ancienneté de l'action de l'homme sur la forêt amazonienne (Roosevelt et al., 1996). Dans le Nord du Pérou, Dillehay et ses collaborateurs (2011) décrivent le développement de l'horticulture puis de l'agriculture chez des chasseurs-cueilleurs à partir de sites vieux de 13.800 à 5000 ans. Des semences de courge domestiquée (*Cucurbita moschata* Duch.) y apparaissent très précocement (10.300 BP). Le portefeuille des espèces cultivées s'élargit considérablement entre 9800 et 7800 BP avec des arachides (8500 BP), un chénopode (quinoa ? 7500 BP), le manioc, des haricots, et le *pacay* (*Inga feuillei* DC.), la *ciruela del fraile* (*Bunchosia* sp.), le coton (*Gossypium barbadense* L. ; 6500 BP) et la coca, espèces dont le statut de domestication n'est pas toujours clair. Il faut cependant noter que nombre d'entre elles proviennent du versant oriental des Andes, ou bien plus au Sud des Andes (chénopode), et même de régions très éloignées (au Sud du bassin amazonien pour le manioc et l'arachide ; probablement de Colombie pour la courge musquée), ce qui implique des distances de contact et d'échange considérables. A partir de 7800 BP, apparaissent même des ouvrages d'irrigation, tandis que ces plantes prennent une grande importance dans l'alimentation : 70% de l'amidon piégé dans les plaques dentaires de neuf individus, âgées de 7800 à 8800 ans, vient de haricots, courge musquée, arachide et pacay (Piperno, 2011).

A partir de données colombiennes, Gnecco (2003) réfute l'image de chasseurs-cueilleurs errant en recherche de nourriture, et soutient au contraire que les paléoindiens avaient un comportement territorial, utilisant les éclaircies sélectives et la replantation, pour concentrer de manière consciente les ressources végétales utiles dès le Pléistocène("forest fields" et "wild orchards"), comme le font encore aujourd'hui les chasseurs-cueilleurs et agriculteurs d'Amérique tropicale (Fedick et Morrison, 2004; Casas et al., 2007; Clement et Junqueira, 2010). Gnecco (2003) présente même des restes archéobotaniques de plantes vraisemblablement domestiquées, dont des semences d'avocat (*Persea americana* Mill.) et d'érythrine (*Erythrina edulis* Triana ex Micheli) vieilles de 10.000 ans. Se référant à plus d'une quarantaine de sites archéologiques, depuis la Colombie jusqu'au Brésil et à la Terre de Feu, Dillehay (1999) étend de tels modèles de gestion des ressources à l'ensemble de l'Amérique du Sud, montrant une grande diversité

technologique et culturelle dès la fin du Pléistocène, dans un contexte de changement climatique et démographique, et d'utilisation et de manipulation accrues des ressources végétales, surtout entre 10.000 et 7000BP. En même temps, se constituent de vastes réseaux d'échange et apparaissent les premiers signes de différenciation sociale. Les premiers cultigènes seraient ainsi apparus entre 10.000 et 8000 BP, voire 12.000 pour des courges domestiquées ou semi-domestiquées (Piperno et Stothert, 2003), bien avant la poterie (7000 BP) et l'architecture monumentale (5000 BP). La gourde-calebasse (*Lagenaria siceraria* (Molina) Standl.) a même été introduite d'Asie à l'état domestiqué, et cultivée en Amérique du Sud depuis plus de 8500 ans (Erickson et al., 2005).

3.1.4. Mésoamérique : un centre de domestication indépendant ?

Au non-centre sud-américain, Harlan (1971) associe le centre mésoaméricain, encore largement admis aujourd'hui (e.g. Piperno, 2011). Pourtant, l'évolution des relations hommes-plantes n'y semble pas fondamentalement différente. Certes, l'agriculture mésoaméricaine s'est développée dans une aire physique bien moins vaste ; et cette aire était, ou plutôt est devenue, le berceau d'une aire culturelle bien définie. Mais aucune étude n'a pu démontrer l'existence d'un foyer de domestication initiale physiquement et culturellement circonscrit dont seraient issus la plupart des cultigènes mésoaméricains et d'où ils auraient ensuite diffusé vers l'ensemble de l'aire mésoaméricaine puis au-delà. Au contraire, on y retrouve quelques sites archéologiques relativement dispersés, témoignant de cultures très anciennes de chasseurs-cueilleurs dont les pratiques de gestion, voire d'horticulture, enclenchent les processus de domestication. Comme en Amérique du Sud, la gourde-calebasse, introduite, était cultivée il y a au moins 10.000 ans au Mexique; elle apparaît avec la courge (*Cucurbita pepo* L.), native, dans les couches les plus anciennes de la grotte de Güilá Naquitz (état d'Oaxaca), alors que les deux autre membres de la "triade" mésoaméricaine, maïs et haricot, seraient originaires des états de Guerrero et Michoacán pour le premier, et de Jalisco pour le second (Smith, 2001). Le maïs, et non plus la téosinte, était déjà cultivé dans le bassin du Río Balsa, il y 8900 ans (Piperno et al., 2009), ce qui indique que la datation de 9000 ans, à partir de la divergence génétique entre les deux formes (Matsuoka et al., 2002), est sous-estimée. La domestication devrait donc dater de 10.000 ans ou d'avantage. En revanche, le haricot semble avoir été domestiqué plus tardivement, les restes les plus anciens appartenant à des formes sauvages. Pour le haricot cultivé, la date mésoaméricaine la plus ancienne est de 2300 ans (Smith, 2001). Datant de 10.000 BP, on trouve encore les premières traces de consommation d'avocat (*Persea americana* Mill.). L'environnement et la quantité de noyaux indiquent que des avocatiers étaient plantés avant 8000 BP, tandis que l'évolution de la taille des cotylédons montre un effet de la sélection pour la taille des fruits, (Smith, 1966, 1968). Le piment (*Capsicum annuum* L.) est déjà distribué dans toute l'aire mésoaméricaine vers 6000 BP. Le coton domestiqué trouvé à Tehuacán (*Gossypium hirsutum* L. ; 5500 BP) avait déjà les caractéristiques des cotons pérennes modernes (Smith et Stephens, 1971).

Comme en Amérique du Sud, la diffusion de ces cultigènes est très précoce. La culture du maïs atteint les basses terres du Sud du Mexique (état de Tabasco) dès 7300 BP, le Panama dès 7800 BP, les Andes de Colombie et d'Equateur dès 7500 BP, l'Amazonie colombienne dès 5800 BP, les Andes péruviennes dès 4000 BP, et même l'Uruguay vers 4700 BP (Pohl et al. 2007), ce qui confirme une date de domestication d'au moins 9000 ans. Nous avons vu que l'avocat est cultivé en Colombie depuis 9500 ans (Gnecco, 2003), alors qu'aucune population sauvage n'a été clairement établie en Amérique du Sud (Coppens d'Eeckenbrugge, recherche en cours). Les données archéologiques et linguistiques sur la présence précolombienne de l'ananas en Mésoamérique (au moins 2500 BP, voire beaucoup plus ; C. Brown, com. pers.) et notre hypothèse de domestication et diffusion de cette plante (section 2.1.) s'inscrivent dans le même schéma général.

Le flux de cultigènes s'établit aussi dans l'autre sens. Le manioc, qui a franchi les Andes dès avant 8500 BP (Dillehay, 2011), apparaît au Panama dès avant 7800 BP et au Mexique (Tabasco) à partir de 5800 BP (Pope et al., 2001). La courge musquée, originaire de Colombie, apparaît dans des strates des sites de Tehuacán (Sud du Mexique) datées de 5500 à 7200 ans (Smith, 1968). Plus tardif, mais très significatif, le cacao, en provenance d'Amazonie, probablement sous une forme non-domestiquée (Clement et al., 2010), est cultivé et consommé dès avant 3750 BP. A une date inconnue, les deux cotons se rejoignent, *G. barbadense* venant du Sud et *G. hirsutum* venant du Yucatán, et commence un processus d'introgression (Stephens, 1973). La liste des cultigènes des deux sous-continents est trop longue que pour l'examiner en détail ici. Quoiqu'il en soit, la double circulation indique que la diffusion des différentes plantes cultivées se fait de manière relativement indépendante, autrement dit qu'elle est d'avantage liée à des échanges de plantes entre peuples qu'à la migration de ces peuples (Dickau et al., 2007). L'Amérique Centrale n'est pas seulement un carrefour entre Amérique du Sud et Mésoamérique. Les nombreux sites anciens et les microfossiles (pollen, phytolythes et grains d'amidon) utilisés pour détecter les traces de plantes domestiquées dans les sites archéologiques (e.g. échantillonnage de pollen dans les lagunes et traces de gestion par le feu) révèlent non seulement que ses basses terres sont occupées par des populations diversifiées tirant une partie de leur subsistance de l'agriculture, mais encore les traces de feux anciens remontant à 11.000 BP révèlent une gestion de la végétation encore plus ancienne, aboutissant à une déforestation relativement avancée (Cooke, 2005; Piperno, 2006).

L'absence de foyer individualisé de domestication et la rapidité de la diffusion des espèces cultivées, domestiquées ou non, suggèrent plutôt un "méga-non-centre" néotropical de domestication et de développement agricole, horticole et agro-forestier, donnant ainsi raison à Brücher (1971, 1987), qui réfutait déjà l'application des hypothèses vaviloviennes à l'Amérique tropicale en soulignant l'importance de la diffusion Sud-Nord, et à McNeish (1967) qui écrivait : "There was no single unilinear development of agriculture in any hearth or hearths but a series of small developments of plant domestication in many regions that stimulated and contributed to the evolution of

agriculture over a wide area". De ce fait, il n'y a pas de raison de se focaliser sur quelques cultigènes majeurs, alors que les espèces, cultivées ou gérées, domestiquées ou non, se comptent par centaines. Au contraire, je tends à penser que cela ne fait qu'ajouter un biais important aux études sur la domestication aux Amériques, et probablement dans d'autres régions tropicales, où il faut résolument prendre en compte la biodiversité initiale, la diversité des interactions plantes-sociétés qui la modifient et la structurent, et étudier l'agro-sylvo-diversité qui en résulte comme une communauté végétale évoluant sous gestion humaine. Comment peut-on comprendre le développement de l'horticulture aux Amériques si on ne garde pas à l'esprit les 1200 espèces fruitières inventoriées aux Amériques (Coppens d'Eeckenbrugge et al., 1998) et la centaine d'espèces commercialisées pour la seule Colombie (niveaux locaux, régionaux et national confondus), ou encore la diversité des tubercules andins ? Et cela même s'il faut en même temps expliquer l'énorme diversité des races de maïs, de pomme de terre, ou les 10 cultivars de haricot commun identifiés dans un site archéologique mexicain vieux de 1500 ans (Smith, 1968).

3.1.4. Prendre en compte les diversités, biologiques et humaines

L'existence de processus quasi-continentaux ("pan-néotropicaux") de domestication et de développement de l'agriculture remet en cause le concept de centre de domestication pour les Amériques et, partant, des approches exagérément focalisées sur un nombre restreint d'espèces annuelles. Comprendre le cas particulier du maïs, aussi important soit-il, ne peut autoriser une compréhension globale des processus passés ni présents. Notre rapide révision souligne au contraire la nécessité de prendre en compte toutes les diversités : diversité des contextes historiques et culturels (mais aussi traits communs, voire propres aux sociétés amérindiennes), diversité des modes de gestion (selon les sociétés ou, en leur sein, selon les espèces gérées et les objectifs de production), diversité des communautés végétales, biodiversité et agrobiodiversité, y compris au niveau infraspécifique.

Il faut reprendre les données de la paléoethnobotanique en essayant d'intégrer les facteurs, biologiques et sociaux, éventuellement environnementaux, dans des modèles portant sur des durées cohérentes avec celles les processus liés à la domestication et à la diffusion des cultigènes. On peut en attendre des informations sur la structuration et le maintien des ressources végétales, leurs migrations anciennes, leur contribution au développement, voire à l'éclosion, de civilisations originales, leurs adaptations aux changements climatiques du passé. Ainsi, l'étude des principales plantes des anciennes civilisations de Mésoamérique doit-elle nous amener à investiguer plus ou moins directement l'importance et l'ancienneté des introductions de plantes sud-américaines dans la région, leur contribution en terme de diversité et d'adaptation des systèmes de production, ou encore une éventuelle modification de leur distribution au cours de la seconde moitié de l'Holocène, en fonction des accidents climatiques, dont certains ont été associés à des catastrophes sociales (e.g. déclin de certaines sociétés Maya). Notamment, les trois à quatre derniers millénaires ont vu une forte intensification de l'agriculture mésoaméricaine, liée à des démographies humaines très dynamiques, et peut être corrélée, déjà, avec une perte relative de sa diversité végétale. La compréhension de ce

passé peut nous aider à répondre aux questions cruciales posées par le changement climatique et les objectifs affichés d'une "intensification écologique" de l'agriculture. Mon ambition n'est évidemment pas de m'attaquer à l'ensemble de ces problématiques, mais de contribuer à ce "dialogue" entre les données anciennes et modernes, par une approche intégrant les sciences de la société, l'histoire et la biologie évolutive.

L'étude d'une si importante biodiversité doit évidemment comporter une phase de compilation, pour commencer à ébaucher une mosaïque montrant la grande diversité des situations, en fonction des plantes, de leurs écosystèmes d'origine, de leur mode de reproduction et de propagation, des sociétés avec lesquelles elles ont co-évolué initialement, de leur utilité potentielle pour ces sociétés, puis pour celles qui les ont ensuite adoptées et adaptées à leurs propres fins. Pour cela, il faut revenir à l'approche proposée par De Candolle (1886). Il faut s'attacher à la diversité biologique du matériel initial (études systématiques), identifier les ancêtres sauvages (démarche seulement en voie d'aboutissement dans le cas du maïs), les distinguer des formes régressives, férales ou rudérales, connaître et comprendre la distribution des unes et des autres, et donc connaître leur écologie et leur écophysiologie, notamment pour reconnaître ce qui est lié à la mise en culture de ce qui est lié à la domestication. Il faut en étudier la diversité phénotypique et la biologie de la reproduction, sexuée et/ou végétative, pour comprendre comment elles ont pu répondre à la sélection et éventuellement être manipulées dans un processus de domestication. Du côté humain, il faut évidemment en passer par l'archéologie, mais aussi par l'ethnographie, historique ou actuelle, qui est indispensable pour interpréter les découvertes archéobotaniques. Ainsi, comment peut-on étudier objectivement, sans être contraint par le modèle occidental (lui-même idéalisé), une transition entre collecte et agriculture, si on ne reconnaît pas dans des pratiques encore très actuelles de nombreuses populations rurales, un travail de domestication "in situ" par enrichissement conscient des jachères et espaces "peu anthropisés" en espèces utiles, avec sélection et propagation des individus ou clones recherchés (Casas et al., 2007) ? Enfin, il faut s'appuyer sur la linguistique comparative historique, même si cette dernière peut présenter des limitations spécifiques, notamment sur la durée longue. Si les linguistes peuvent détecter les sources d'erreurs potentielles liées aux sens multiples des mots, à leur construction et aux emprunts entre langues, il semble très difficile, voire impossible, de remonter dans le passé très lointain, pratiquement au-delà de 7000 ans (Brown, 2010). La linguistique peut donc nous aider à tracer la diffusion d'un cultigène, mais on ne peut en attendre qu'elle nous fournisse des clés pour les premiers développements de l'agriculture et les domestications qui remonteraient bien au-delà de cette date. En revanche, les langues constituant une composante essentielle de l'identité sociale, elle peut nous éclairer sur les relations entre sociétés et agrobiodiversité. Notamment, la transmission sur le temps long des mots relatifs à une plante est liée directement à son importance durable pour les sociétés concernées. La linguistique nous permet ainsi de constituer de manière objective des sous-échantillons des espèces les plus importantes et caractéristiques de l'agrobiodiversité exploitée par un groupe humain et de suivre sa diversification au cours du temps et des processus de différentiation sociale/linguistique.

3.2. Axes de recherche développés

Je propose ainsi de développer mes recherches autour de trois axes principaux : i) la structuration sociale des ressources génétiques ; ii) la diversité linguistique et la distribution des anciens agro-systèmes ; iii) l'origine, les distributions, les niches écologiques et la diversité et domestication des espèces cultivées.

3.2.1. Structuration sociale des ressources génétiques : le modèle G x E x S

La réflexion théorique initiée avec Christian Leclerc et Fabrice Sagnard au début du projet ATP "Reproduire une plante, reproduire une société" a fait l'objet d'un article de synthèse proposant un nouveau modèle d'étude (Leclerc et Coppens d'Eeckenbrugge, 2012). Après une révision des études de génétique des populations cultivées de sorgho et maïs, et de leurs limitations, nous y avons analysé pourquoi la diversité génétique des cultures ne peut être étudiée sans une approche anthropologique qui prenne en compte l'identité culturelle des paysans et les réseaux sociaux. Les cultivars sont alors considérés comme des objets sociaux, dépendant des systèmes de classification paysans. Parce que l'adoption d'une semence implique un haut degré de confiance, les flux de semences sont orientés de manière centripète en fonction de l'identité sociale des acteurs. Ainsi, les semences, tout autant que les traits culturels, sont soumises aux processus de transmission verticale (vs. les processus horizontaux de diffusion), eux-mêmes déterminés par les règles qui organisent les sociétés rurales (résidence, mariage, héritage). La forte analogie entre la différenciation culturelle des fermiers et la différenciation génétique des plantes cultivées nous a menés à proposer un cadre méthodologique commun pour l'anthropologie sociale et l'application des méthodes de génétique des populations, prenant en compte le facteur social, au-delà de la somme des individus qui composent un groupe, selon un modèle d'interaction G x E x S, où S désigne les facteurs de différenciation sociale. Ce même cadre peut fonctionner dans l'autre sens, les marqueurs génétiques des plantes cultivées pouvant être utilisés comme des marqueurs historiques de relations humaines du passé.

Le modèle G x E x S a été mis en œuvre dans le projet ATP sus-mentionné, dans les projets ARCAD (Agropolis Resource Center for Crop Conservation, Adaptation and Diversity) et ANR-PICREVAT (Prévisibilité de l'information climatique pour la réduction de la vulnérabilité de l'agriculture tropicale). Il a permis non seulement de mettre en relation la diversité des plantes et l'identité culturelle des paysans au niveau intra- et interspécifique (Labeyrie et al., 2013), mais aussi de montrer l'effet du mode de transmission des semences sur l'adaptation climatique des populations cultivées (Mwongera et al., 2013). L'anthropologie sociale éclaire les réseaux d'échanges de semences de manière originale en caractérisant les organisations sociales, notamment par les taux d'intermariage parmi des unités sociologiques discrètes. Les effets structurants d'une orientation centripète des échanges (conclus davantage à l'intérieur qu'entre les groupes sociaux) sont cumulatifs à mesure que des niveaux supérieurs d'intégration sociologique sont considérés.

Le modèle G x E x S rend possible une analyse multiscalaire avec un passage progressif des niveaux inférieurs et locaux vers les niveaux supérieurs et globaux. Le modèle possède ainsi l'avantage de concilier une caractérisation de la diversité à grande échelle de temps et d'espace (plus familère dans les études portant sur la domestication) avec l'étude des mécanismes sociologiques qui peuvent être décrits et analysés à une échelle plus locale. Par exemple, une reconstitution des voies de diffusion du bananier depuis l'Asie du Sud-Est vers l'Afrique de l'Est (Perrier et al., 2011) s'est avérée possible parce que, localement, le long du tracé, les ressources génétiques qui ont été collectées et caractérisées ont conservé l'empreinte génétique liée à leur introduction initiale il y a plusieurs centaines d'années. Si un brassage continuel des ressources génétiques cultivées s'observait, de proche en proche, entre les groupes sociaux humains (diffusion horizontale), aucune reconstitution à grande échelle ne serait possible. Le modèle G x E x S, en somme, suppose l'existence de barrières sociales qui organisent les flux de gènes via les semences. Cette force évolutive est donc de nature non seulement biologique, mais également sociale.

3.2.2. Diversité linguistique et distribution des anciens agro-systèmes

Non seulement les gènes mais aussi les plantes elles-mêmes peuvent fournir des marqueurs du passé. Leur nom dans les langues indigènes est hérité des sociétés passées selon un schéma vertical semblable à un arbre phylogénétique, et leur évolution peut être reconstruite jusqu'aux époques où l'agriculture s'est imposée comme source essentielle de nourriture, et même au-delà. L'idée d'étude paléobiolinguistique de Cecil Brown est d'inférer les mouvements des sociétés agricoles à partir de l'évolution du portefeuille des principales espèces contribuant à leur subsistance. Cette idée inverse en quelque sorte le principe de l'étude de la diffusion des plantes par la transmission et la distribution de leurs noms, principe appliqué notamment aux plantes introduites en Afrique de l'Ouest (Bahuchet et Philippson, 1998; Blench, 2009).

Dans la collaboration avec Cecil Brown, nous utilisons les mêmes méthodes que pour la cartographie des ressources génétiques pour localiser les régions où a pu se développer l'agriculture de certaines familles linguistiques à partir de l'Holocène moyen. Nous nous sommes d'abord intéressés à la famille otomangue et, plus particulièrement sa branche zapotèque pour tester la méthode. Nous en donnons ici des résultats préliminaires et très généraux, à titre d'exemple d'application de la méthode.

Parmi les peuples de la sphère culturelle mésoaméricaine, les Otomangues constituent le groupe linguistique non controversé le plus ancien (> 6500 BP) et le plus clairement associé à une agriculture déjà diversifiée. Ils ont été associés à la culture dite de Tehuacán, dont l'étude archéologique a permis d'identifier nombre d'espèces pour lesquelles des mots otomangues très anciens peuvent être reconstruits. Une étude géographique de la distribution des quatre plus anciennes branches de la famille otomangue nous indique qu'elles ont vraisemblablement diffusé à partir d'une zone contigüe à la vallée de Tehuacán et au centre de plus grande diversité lexicale des langues otomangues actuelles. Ainsi, cette première approche phylogéographique nous indique

que centre d'origine et centre de diversité concordent pour cette famille linguistique. Cecil Brown a pu vérifier la reconstruction des noms de six espèces cultivées pour cette famille : avocat, piment, coton, manioc, maïs et tabac ; deux autres plantes sont des candidats moins sûrs : le sapote mamey (*Pouteria sapota* (Jacq.) Moore & Stearn) et l'ananas. A partir de la modélisation des niches écoclimatiques de chacune de ces espèces à l'Holocène moyen, nous pourrons analyser leur distribution potentielle conjointe dans la région d'origine de la famille otomangue. Nous devrions ainsi pouvoir tester la cohérence de l'ensemble des informations sur la distribution de la société otomangue ancestrale et des plantes les plus importantes de son agrobiodiversité.

Les Zapotèques, qui descendent des Otomangues, ont hérité de cette agriculture diversifiée et l'ont développée plus avant, essaimant leurs groupes dialectaux dans toute la moitié sud de l'Isthme de Tehuantepec (état d'Oaxaca). Leurs locuteurs actuels y étant relativement bien localisés, nous attendions des résultats relativement simples. En fait, les résultats préliminaires de l'étude, couplés à nos nouvelles données sur l'origine géographique des Otomangues, indiquent une migration relativement importante de la branche zapotèque.

3.2.3. Distribution, niches écologiques, diversité et domestication des espèces cultivées

Poursuite des travaux sur la domestication des passiflores en relation avec leur diversité

Les passiflores fournissent un bon modèle d'un groupe hautement diversifié ayant fourni un nombre remarquable de cultigènes, eu égard à leur importance économique et aux difficultés que l'on peut concevoir dans la gestion durable de lianes ligneuses. Nous avons vu que les nombreuses passiflores domestiquées trouvent préférentiellement leur origine au sein de groupes d'espèces morphologiquement homogènes (grande diversité d'espèces autour d'un patron morphologique bien défini), où l'on observe des endémismes étroits, plutôt que chez des espèces très polymorphes présentant des aires de distribution beaucoup plus larges, grâce à leur plasticité écologique. Il semble donc exister une relation entre la structuration de la diversité entre les espèces, leur tendance à l'endémisme et/ou le potentiel de domestication.

Dans le cadre d'une collaboration avec Laurence Pascal (UMR CEFE puis UMR DIADE) sur la diversité fruitière en Guyane, nous avons débuté une étude sur l'un des ces groupes, les *Laurifoliae*, comptant deux espèces domestiquées, *P. nitida* Kunth et *P. laurifolia* L. L'étude, qui avait donné lieu au stage de Mastère de Maxime Rome, a repris récemment, lorsque ce dernier a été engagé au Jardin Botanique de Lyon. Elle comporte un volet taxonomique, avec une révision approfondie de l'évolution de la taxonomie dans le groupe, en Amérique tropicale humide ; et une étude systématique, basée sur la caractérisation des diversités morphologique et génétique, aux niveaux intra- et interspécifique, au moins en Guyane. Enfin, la caractérisation des niches éco-climatiques des différentes espèces, validées par l'étude systématique, devrait permettre de mieux comprendre une telle radiation d'espèces si proches dans leur morphologie et dans leurs caractères écologiques les plus apparents. Nous en attendons également qu'elle permettra

de confirmer un lien entre endémisme et potentiel pour la domestication et d'éclaircir la relation entre l'espèce cultivée aux Antilles (introduction précolombienne) et ses parents sauvages du continent.

Plantes domestiquées d'importance économique et culturelle particulière

La réunion et la validation d'ensembles de données pour modéliser la distribution des principales espèces définissant la "niche agricole" d'anciens groupes ethnolinguistiques mésoaméricains nous a déjà permis de développer une expérience conséquente sur la distribution des formes sauvages et domestiquées de ces espèces. Ainsi, outre l'intérêt de la méthode paléobiolinguistique pour l'étude des sociétés préhistoriques, cette recherche apporte également une information intéressante pour la domestication des plantes mésoaméricaines et sur l'introduction et la diffusion précoces de plantes sud-américaines (ananas, goyaves, manioc, tabac, cacao, entre autres).

Pour certaines questions, notamment la relation entre plantes sauvages et plantes domestiquées ou la diffusion de ces dernières, ou encore, inversement, les effets de la diffusion sur la domestication, l'apport des méthodes de modélisation de niches écoclimatiques peut être particulièrement éclairant. La prise en compte du statut spontané ou cultivé des spécimens utilisés permet non seulement d'apprécier la qualité des modèles de distribution, mais aussi d'étudier les effets de la domestication sur cette distribution. La relation entre domestication et extension de l'aire de répartition d'une espèce a été peu étudiée. Pourtant, lorsqu'il est possible de différencier les formes cultivées des formes rudérales et férales, voire sauvages lorsqu'elles existent encore, cette relation peut s'avérer hautement informative.

Par exemple, la distribution naturelle du coton mésoaméricain, *G. hirsutum*, a longtemps fait débat, certains experts ayant même nié pendant longtemps la persistance de populations sauvages (Hutchinson, 1951). Actuellement, l'hypothèse la plus communément admise est que la domestication du cotonnier a eu lieu dans le Nord du Yucatán où la population littorale serait sauvage et non férale (Brubaker et Wendel, 1994; Pearsall, 2008; Piperno, 2011). Jusqu'à présent, l'étude génétique et physiologique des effets de la domestication a donc été basée sur cette seule population (Butterworth et al., 2009 ; Rapp et al., 2010).

La comparaison des paramètres climatiques liés à la distribution des cotonniers pérennes sauvages et féraux montre que la plus large distribution de ces derniers est essentiellement liée à la perturbation des milieux. Les populations férales ne se perpétuent que lorsqu'elles restent associées à la perturbation et aux populations cultivées "d'origine". Ainsi, même à l'état féral, le cotonnier domestiqué reste subordonné à l'homme. Il apparaît que le facteur limitant est, tout comme pour le cotonnier sauvage, son incapacité à supporter la compétition lorsque le milieu commence à se refermer. Et, précisément, ce sont les paramètres rigoureux de l'enveloppe climatique des populations sauvages qui définissent les rares écosystèmes au sein desquels la compétition est faible ou inexistante (e.g. plages arides soumises aux embruns). La niche climatique correspond donc bien à une niche écologique. Et même s'il est résistant au sel et à l'aridité, un

cotonnier domestiqué, dont les graines ont perdu leur dormance, ne peut y fonder de descendance durable.

Cette modélisation de la niche écologique des populations littorales confirme le statut sauvage de la population littorale au Nord du Yucatán, mais aussi de nombre de populations de l'Est Caribbéen, des Bahamas et de la Floride, lesquelles se maintiennent dans les mêmes conditions d'aridité extrême. Or, les chroniques coloniales mentionnent que les populations amérindiennes des Caraïbes y pratiquaient et la collecte de cotonniers sauvages et la culture de cotonniers pérennes, en jardin de case ou en parcelle de plein champ, selon la qualité de coton recherchée (Stephens, 1965). L'existence d'autres populations littorales sauvages pose donc la question d'une éventuelle domestication de *G. hirsutum* au Vénézuéla et/ou aux Antilles. La question est complexe, dans la mesure où l'espèce y est essentiellement représentée par la race 'marie-galante', race particulièrement résistante à la sécheresse et issue d'introgression avec le cotonnier sud-américain, *G. barbadense*. Ce n'est que lorsque cette dernière espèce, déjà domestiquée, a diffusé jusque dans la Caraïbe que la race 'marie-galante' a pu se former à partir d'une contribution maternelle (*G. hirsutum*) sauvage et/ou domestiquée. Notre première étude permettra d'optimiser l'échantillonnage de populations sauvages et cultivées dans les collections pour tester prochainement les différentes hypothèses par une analyse génétique, en collaboration avec Jean-Marc Lacape (UMR AGAP).

Un autre avantage de l'utilisation de la méthode provient de la possibilité d'extrapoler les modèles aux climats du passé, par exemple ceux du Pléistocène, ce qui apporte une information importante pour les plantes de domestication très ancienne.

D'autres plantes que celles mentionnées pour l'étude paléobiolinguistique pourront être étudiées de la même manière. Ainsi commencerons-nous bientôt une collaboration avec le réseau COGENT pour établir la distribution du cocotier et celle de sa diversité, en espérant trouver dans le modèle climatique des indications sur l'aire de distribution originelle de ce palmier de première importance pour de nombreuses populations des côtes tropicales. De nombreuses autres collaborations sont envisagées, la place de Montpellier étant particulièrement favorable, de par la concentration d'expertise et de bases de données que l'on peut y mobiliser.

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Stephens, S.G. 1973. 16. Geographical distribution of cultivated cottons relative to probable centers of domestication in the New World. In: Adrian, M.S.: Genes, enzymes, and populations. 239-254.

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Todou, G., Benoit, L., Gabeloux, M., Roux, E., Coppens d'Eeckenbrugge, G., Joly, H. 2010. Structure et dynamique de la diversité génétique dans des populations cultivées et spontanées de deux espèces de *Dacryodes (*Burseraceae) au Cameroun et au Gabon. Colloque de Restitution du projet IFORA, Montpellier, June 22-23.

Van Droogenbroeck, B., Breyne, P., Goetgebheur, P., Romeijn-Peeters, E., Kyndt, T., Gheysen, G. 2002. AFLP analysis of genetic relationships among papaya and its wild relatives (Caricaceae) from Ecuador. Theoretical and Applied Genetics 105: 289-297.

Van Droogenbroeck, B., Kyndt, T., Romeijn-Peeters, E., Van Thuyne., W., Goetghebeur, P., Romero-Motochi, J.P., Gheysen, G. 2006. Evidence of natural hybridization and introgression between *Vasconcellea* species (Caricaceae) from southern Ecuador revealed by morphological and chloroplast, mitochondrial and nuclear DNA markers. Annals of Botany 97:793-805.

Yockteng, R., Coppens d'Eeckenbrugge, G., Souza-Chies, T.T. 2011. *Passiflora* L. In Kole, C. (ed.) : Wild crop relatives: genomic and breeding resources. Tropical and subtropical fruits. Springer Verlag, Berlin, Heidelberg, 129-171.

Yockteng, R., Nadot, S. 2004. Phylogenetic relationships among *Passiflora* species based on the glutamine synthetase nuclear gene expressed in chloroplast (ncpGS). Molecular Phylogenetics and Evolution 31, 379-396.

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ANNEXES

UNIVERSITÉ CATHOLIQUE DE LOUVAIN

FACULTÉ DES SCIENCES AGRONOMIQUES

Nous, Recteur de l'Université Catholique de Louvain;

Vu le règlement organique de l'Université et celui de la Faculté des Sciences Agronomiques;

Attendu qu'il résulte des déclarations faites par Messieurs les Président et Membres du Jury de cette Faculté;

que M. Monsieur Geo Coppens d'Eeckenbrugge, né à Bukavu (Zaire), le 24 septembre 1957, est porteur d'un diplôme de Ingénieur agronome délivré par l'Université Catholique de Louvain le 22 janvier 1981 et des pièces établissant qu'il a satisfait aux dispositions des règlements ci-dessus mentionnés;

Attendu qu'il a présenté une dissertation originale intitulée Relations pollen - pistil chez la chicorée (Cichorium intybus L.)

Attendu qu'il a défendu publiquement cette dissertation avec la plus grande distinction

Avons conféré et conférons à M. Monsieur Geo Coppens d'Eeckenbrugge le grade de DOCTEUR EN SCIENCES AGRONOMIQUES.

En foi de quoi, nous lui avons délivré le présent diplôme, signé par Nous, par Messieurs les Président et Membres du Jury et par Monsieur le Secrétaire Général de l'Université.

Fait à Ottignies-Louvain-la-Neuve, le 23 juin 1987

Le Secrétaire Général de l'Université,

Signature du porteur,

Le Recteur de l'Université,

Le Président du Jury,

Les Membres du Jury,

CURRICULUM VITAE

Geo COPPENS d'EECKENBRUGGE

French, born in Pweto (DR Congo), September 26th 1957
Married, five children

Office address : CEFE, 1919 Route de Mende, 34393 Montpellier Cedex 5.
Telephone : (33)4 67 61 32 99 (office), (33)4 67 55 39 31 (private) ;
Fax : (33)4 67 61 71 47
e-mail : /

Diplomas:

Baccalauréat Série C (Mathematics and Physics)
Académie de Montpellier, 1975

Ingénieur Agronome (orientation Tropical and Subtropical Agronomy)
Université Catholique de Louvain, 1981
Grade : Grande Distinction
Engineer thesis : Ressemblance phénotypique des jumeaux et héritabilité en fonction de l'âge parental (*twin phenotypic correlation and heritability as a function of parental age*)

Docteur en Sciences Agronomiques
Université Catholique de Louvain, 1987
Grade : La Plus Grande Distinction
Thesis : Relations pollen-pistil chez la chicorée (*Cichorium intybus* L.) (*Pollen-pistil interactions in chicory*)

Scientific awards:

Prix Joseph Schepkens (1984-1987 : Research in Agronomy)
Académie Royale des Sciences de Belgique

Alfred H. Krezdorn Award (2000), for the best communication in fruit research, Interamerican Society for Tropical Horticulture.

Premio bienal APUCV (Asociación de Profesores de la Universidad Central de Venezuela) al libro de texto universitario, edición 2008, por la obra : La piña de América o ananás

Languages:

French, English, Spanish, Portuguese: fluently spoken and written; **Catalan:** working knowledge; **Italian:** passive knowledge

Areas of expertise:

Plant Genetics and Breeding, Genetic Resources and Agrobiodiversity, Plant Domestication in the Neotropics.

CURRENT POSITION

2005-present: **research on genetic resources and domestication of tropical fruits** at **UMR CEFE**, BioCultural Interactions team.

- **Research on crop genetic diversity, distribution and domestication**, with emphasis on **passion fruit, papaya, and safou** (African plum; *Dacryodes edulis*).

- **Collaborative research**, with anthropologists, **on past and present relations between social differentiation and agrobiodiversity**.

- **Training of students** from the graduate to the doctoral level.

PREVIOUS POSITIONS

1994-2005: **expert in tropical fruit genetic resources** at **CIRAD-FLHOR**, in relation with **IPGRI** (posted at the IPGRI regional office in Cali, Colombia, from 1994 to 2002, and at CIRAD-FLHOR headquarters in Montpellier from 2002 to 2005).

- **Associate coordinator of the subregional networks** REDARFIT (Andean genetic resources) and TROPIGEN (Amazon genetic resources) while based at Cali.

- **Preparation, submission, negotiation, and coordination of** two **international projects**, funded by the EU (pineapple germplasm characterization and evaluation for diversity study and resistance breeding), FONTAGRO (diversity of papayas and their pathogens, and resistance breeding at the interspecific level), and two **Colombian projects**, funded by Colciencias (Andean passion fruit diversity) and the Ministry of Environment (mapping diversity of Passifloraceae and Caricaceae in the coffee growing zone to develop information and tools for more global *in situ* diversity conservation).

- **Technical support** to the project partners and national programme scientists in the region.

- **Research activities** through involvement in project and training activities and inventory of neotropical fruits.

- **Training of students** from the graduate to the doctoral level.

1989-1994: CIRAD-FLHOR Pineapple Programme in Martinique.

- Study of the **pineapple breeding system**.
- Pineapple breeding and **selection of new varieties**
- **Pineapple germplasm collecting, characterization and evaluation**

1981-1989 : Laboratoire de Phytotechnie Tropicale et Subtropicale of the Université Catholique de Louvain (U.C.L.):
October 1985 to April 1989: chicory research on private funds
Octobre 1983 to September 1985: doctoral grantee of the Belgian Institut de Recherche Scientifique pour l'Industrie et l'Agriculture
March 1981 to September 1983: chicory research funded by the Fonds de Développement Scientifique

Areas of research at U.C.L.:

- **breeding system of chicory** (*Cichorium intybus* L.)
- **Brussels chicory breeding** to develop a methodology for cultivars adapted to hydroponic forcing
- Study of **parameters related to inulin and fructose yield in industrial chicory**, at the diploid and polyploid levels
- **Industrial chicory breeding** to improve inulin yield and quality
- Study of **reproduction in black salsify** (*Scorzonera hispanica* L.)
- **Study of breeding system in the genus *Brachiaria*** (tropical forage grasses) to **transfer apomixis** through interspecific hybridization.
- Reconstitution of synthetic populations of maize in Central Africa (Congo).

Teaching charges at U.C.L. (1987-1989):

- Participation in seminars of Horticultural Plant Ecophysiology (student work monitoring)
- Part of the Plant Breeding lessons (on breeding systems)
- Direction of theses at graduate and postgraduate levels
- Participation in the supervision of a doctoral thesis

PUBLICATIONS AND COMMUNICATIONS

- 27 articles in refereed international journals
- 51 articles in other journals
- 1 book
- coedition of one book (workshop proceedings)
- 27 book chapters
- 62 communications and conferences in congresses and courses
- a web site on taxonomy and ethnobotany of American fruits from 2001 to 2011.

INDIVIDUAL TRAINING

Supervision of students:

- 24 at the graduate and postgraduate levels
- 3 at the doctoral level

REFEREE

Manuscript reviews for Plant Genetic Resources Newsletter, Euphytica, Fruits, Cahiers de l'Agriculture, New Zealand Journal of Botany, Journal of the American Society for Horticultural Science, Acta Horticulturae, and Plant Cell Reports.

Web page review for the Global Invasive Species Database (Member of the Invasive Species Specialist Group of the World Conservation Union - IUCN).

ASSOCIATE EDITOR

Revista Brasileira de Fruticultura

MEMBERSHIP

International Society of Ethnobiology

PARTICIPATION IN INTERNATIONAL SCIENTIFIC MEETINGS

- Symposium : Cellular and Molecular Aspects of Reproduction in Higher Plants, Liège (Belgium), May 8 1981.
- 7ème Biennale de l'Endive. Beauvais (France), October 7-8 1985.
- Colloque EUCARPIA sur les Légumes à Feuilles. Versailles (France), February 28 - March 2 1984.
- Symposium "Biotechnology and Ecology of Pollen". Amherst (Massachussets, U.S.A.), July 8-11 1985.
- 9ème Colloque International de Cytobiologie de la Reproduction Sexuée des Plantes Supérieures. Reims (France), September 16-18 1986.
- EUCARPIA Congress: Genetic Manipulation in Plant Breeding - Biotechnology for the Breeder. Elsinore (Denmark), September 11-16 1988.
- Symposium : Biotechnologies pour le Développement de la Caraïbe. Fort-de-France (Martinique), November 27 - December 1 1989.
- 23d International Horticultural Congress. Florence (Italy), August 27 - September 1 1990.
- XIIth Eucarpia Congress. Angers (France) : July 6-11 1992.
- International Pineapple Symposium. Honolulu (Hawaï, U.S.A.), November 2-6 1992.
- Primer Simposio Latinoamericano de Piñicultura. Cali (Colombie), May 25-29 1993 (invited conference).
- IICA-CIRAD/FLHOR Regional Workshop on Pineapple Production. Fort-de-France, (Martinique), March 20-22 1994 (invited conference).
- 2d Symposium International Ananas. Trois-Ilets (Martinique), February 20-24 1995.
- Simposio Internacional de Estadísticas en Agricultura y Medio Ambiente, CIAT, Palmira (Colombia), June 7-9 1995.
- Primer Simposio Internacional sobre Fruticultura Tropical y Subtropical. La Habana (Cuba), September 26-29 1995.
- Simposio CIRAD/CATIE - Mejoramiento Genético y Desarrollo de los Cultivos Tropicales. Turrialba (Costa Rica), November 20-29 1995.
- Consultation on the Management of Field and In Vitro Genebanks. CIAT, Cali (Colombia), January 15- 20 1996.
- Réunion EUCARPIA sur les plantes tropicales, Montpellier (France), March 11-15 1996.
- IIIa Reunión de Investigadores del Piedemonte Amazónico, Florencia (Colombia), May 29-31 1996 (invited conference).
- XLIV Annual Meeting of the Interamerican Society for Tropical Horticulture, Barquisimeto (Venezuela), September 28- October 2 1998 (invited conference).
- Third International Pineapple Symposium, Pattaya (Thailand), November 17-20 1998.
- II Simposio de Recursos Genéticos para América Latina y el Caribe. Brasilia, November 21-26 1999.
- XLVI Annual Meeting of the Interamerican Society for Tropical Horticulture,

Miami (Florida, USA), September 24-29 2000.

- Fourth International Pineapple Symposium, Veracruz (Mexico), April 16-19 2002 (Member of the Scientific Committee).
- X Seminario Nacional y IV Internacional sobre Especies Promisorias. Universidad Nacional de Colombia, Medellín, October 29-31 2003 (invited conference).
- L Annual Meeting of the Interamerican Society for Tropical Horticulture, Limón (Costa
- Rica), October 23-29 2004.
- Fifth International Pineapple Symposium, Port Alfred (South Africa). April 11-15, 2005 Member of the Scientific Committee).
- Evolutionary Genomics, Banyuls-sur-Mer (France), October 26-28 2005.
- First International Symposium on Papaya. Papayas for the World. Genting Highlands (Malaysia), November 22-24, 2005
- Diversitas First Open Science Conference, Oaxaca (Mexico), November 9-12 2005.
- Le Réveil du Dodo II. Journées francophones des Sciences de la Conservation de la Biodiversité. Paris, March 7-9 2006.
- XXXe Rencontres Iinternationales d'Archéologie et d'histoire d'Antibes. Des hommes et des plantes. Exploitation du milieu et gestion des ressources végétales de la Préhistoire à nos jours. Juan-les-Pins, October 22-24 2009
- XIIIth International Congress of Ethnobiology, Montpellier (France), May 20-25 2012 (**member of the organizing team**).

MOST RELEVANT DUTY TRAVELS

- September 10-15 1985: representation of UNIBRA at the Board of the U.S. Agricultural Development Corporation in Washington.

- January 8-28 1986: travel for the GENAGRO (NGO) in Congo, including :
- 15 to 18: exploratory mission at Idiofa for the Compagnie Commerciale du Bandundu.
- 21 to 25: exploratory mission at Kongolo and Kalemie (North Katanga) for ESTAGRICO.

- April 8-28 1991: supervision of the pineapple breeding program in Côte d'Ivoire.

- May 12-15 1991: pineapple chapter (biology and production factors) of the Regional Course on Tropical Fruit Production for Export at the U.W.I. (University of West Indies), Port-of-Spain (Trinidad).

- September 11- October 18 1992: collecting wild and cultivated pineapple germplasm in Brazil (states of Acre and Mato Grosso).

- March 22-April 23 1993: collecting wild and cultivated pineapple germplasm in French Guiana.

- September 17-28 1993: representation of CIRAD-FLHOR at the PROCITROPICOS meeting for the constitution of TROPIGEN (network for phytogenetic resources of the Amazon region) in Brasilia and meetings on pineapple genetic resources and breeding at EMBRAPA-CENARGEN and EMBRAPA-CNPMF (Bahia).

- November 14 - December 17 1993: collecting wild and cultivated pineapple germplasm in Brazil (state of Amazonas).

- November 20- December 1 1994: travel to Brazil (Brasilia and Salvador) to prepare an international project for the characterization and evaluation of pineapple genetic resources.

- February 12-19 1995: travel to Venezuela to prepare an international project for the characterization and evaluation of pineapple genetic resources.

- September 26- October 7 1995: Study of a project on pineapple genetic resources in Cuba, completed by a quick review of the Cuban pineapple breeding program.

- October 15-17 1996: representation of CIRAD-FLHOR at a CIRAD-ORSTOM-INRA/EMBRAPA meeting to coordinate cooperation activities with EMBRAPA centers.

- November16- December 1 1996: study of passion fruits in Brazil (genetic resources, breeding, research, industry).

- December 1-5 1996: identification of potential projects on fruit genetic resources, Lima (Peru).

- January 30- February 10 1997: Study of Andean passionfruits in Ecuador.

- October 1st 1999. Conference on the application of biotechnology in neotropical fruit breeding, in the framework of the training course "Biotecnologías aplicadas a la conservación y al mejoramiento de los recursos genéticos de los cultivos marginados nativos de América Latina", co-organized by the Instituto Italo-Latinoamericano (Italian cooperation) and the Pontificia Universidad Javeriana in Bogota (Colombia).

- March 26-30 2001: Teacher on tropical fruit breeding at the Curso de Fruticultura Tropical, training course organized by the Agencia Española de Cooperación Internacional (Spanish cooperation agency), Cartagena de Indias (Colombia).

- July 28- August 7 2002: Study of wild papayas in Costa Rica.

- January 30- February 12 2006: Study of the African plum (*Dacryodes edulis*) in Cameroon.

- March 25-April 11 2008 : field study of genus *Passiflora* subgenera *Distephana* and *Passiflora/Laurifoliae* in French Guiana.

- November 11-December 9 2009: Botanical expedition for collecting samples of *Dacryodes* and other rain forest tree species in Western Cameroon.

MAIN PROJECTS PREPARED, SUBMITTED AND COORDINATED

- **Evaluation and utilization of pineapple genetic resources from the Amazon to breed resistant varieties**. Five-year international project funded by the **EU-INCO programme**, involving CIRAD-FLHOR in Montpellier and Martinique (**France**), Universidade do Algarve (**Portugal**), Instituto Nacional de Investigación Agronómica (**Venezuela**), EMBRAPA - Biotecnologia e Recursos Genéticos and EMBRAPA-Mandioca e Fruticultura (**Brazil**), **1997-2001**.

Objective: characterization, evaluation and selection for direct use and/or breeding, with particular emphasis on resistance to the main pineapple pathogens.

- **Conservación y utilización de recursos genéticos de pasifloras** (*Conservation and utilization of passiflora genetic resources*). Three-year **Colombian project** funded by Colciencias, involving **CENICAFE**, the **Pontificia Universidad Javeriana** of Bogota and the **CIRAD-IPGRI** group, **1999-2001**.

Objective: Characterization (including cytogenetics), evaluation and selection of promising genotypes, development of germplasm conservation techniques and diversity study.

- **Aprovechamiento de los recursos genéticos de las papayas para su mejoramiento y promoción** (*Utilization of papayas genetic resources for their improvement and promotion*). **Regional project** funded by **FONTAGRO**, involving national institutions from **Venezuela** (Instituto Nacional de Investigación Agronómica, Universidad Central de Venezuela, IVIC, Centro Nacional de Conservación de los Recursos Fitogenéticos), **Colombia** (CORPOICA, Universidad Nacional, Universidad de Caldas), **Ecuador** (Instituto Nacional de Investigación Agropecuaria, Universidad Técnica de Ambato), **Costa Rica** (Universidad de Costa Rica), **CIRAD-FLHOR**, **CIAT**, and **IPGRI**, **1999-2003**.

Specific objective : Germplasm collecting, characterization and evaluation, study of the diversity of common papaya and moutain papayas and their main pathogens, study of host-pathogen genetic interaction, breeding at the interspecific level for resistance transfer.

- Estudio de la diversidad de las Passifloraceae y Caricaceae en la zona cafetera (diversity of Passifloraceae and Caricaceae in the coffee growing zone). **Colombian project**, funded by the **Ministry of Environment**, involving **CENICAFE** (Centro Nacional de Investigación del Café), **IPGRI** and **CIRAD-FLHOR**, **2003-2005**.

Specific objective : Study of the distribution of wild and cultivated passifloras and mountain papayas, diversity mapping (in relation with that of ants and birds studied in a parallel project), in a composite landscape of forest patches and cultivated areas of varying diversity, along the Colombian Andes. Comparison with historical and herbarium data. Identification of local and global factors of major impact on taxonomic diversity (climate change, relation between agrobiodiversity and global diversity, fragmentation, local conservation policies).

INDIVIDUAL TRAINING ON PLANT GENETIC RESOURCES RESEARCH AT IPGRI AND CIRAD

Barney, Victoria E. (Colombian) 1995-2000
Diversity of banana passion fruits and their wild relatives (U. Nacional, PhD thesis, discontinued because of funding cuts).
Vicky Barney has resumed research activities on Passiflora, getting funds from the New Zealand government and identifying predators of P. tarminiana *to fight against this species, which is invasive in these islands.*

Barrera, Carlos Felipe (Colombian) 2001-2002
Morphological characterization of passion fruits (engineer thesis, U. Caldas)

Clavijo, Fernando (Colombian) 2012
Etude phylogéographique du genre *Dacryodes* au Cameroun et au Gabon (MSc thesis, University of Montpellier 2, year 2)

De La Torre, Claudia (French) 2001
Ethnobotanic study of fruit diversity and utilization in a community of the Upper Amazon (graduate thesis, Centre National d'Etude Agronomique des Régions Chaudes, in collaboration with Prof. Sandra Noda, INPA, Manaus)
Since 2001, Claudia De La Torre has worked in institutions providing technical support for tropical horticulture, mostly in French oversea territories.

Farfán Lina Clemencia (Colombian) 2001
Morphological characterization of passion fruits (engineer thesis, U. Caldas)

Garcin François (French) 2001-2002 (voluntary training), 2002-2003 (as a student)
Analysis of morphological diversity of Andean passion fruits in Venezuela, Colombia, Ecuador, Peru and Bolivia (MSc thesis, EPHE).

Jiménez Daniel R. (Colombian) 2001-2002
Isozyme diversity in papaya and mountain papayas from Costa Rica, Ecuador and Colombia (engineer thesis, U. Caldas).
Daniel Jiménez has carried out his doctoral research on sugar cane yield modeling in Basel (Switzerland), and collaborated with CIRAD in Montpellier and La Réunion. He is currently working at the Land Use unit of the Centro Internacional de Agricultura Tropical, Cali, Colombia.

Klimes Anna (Canadian) 1999-2000
Morphological characterization of passion fruits and diversity study on herbarium material (voluntary training)
Anna Klimes wrote me that her Colombian field research experience helped her in applying for a PhD in Cell Biology. In 2010, she was appointed at the University of Western New England (USA, Mass.) as an Assistant Professor in Biology.

Komba Mayossa, Prune (Gabonese) 2013 (May-September)
Etude de la distribution du cocotier et de sa diversité (MSc I, Université de Versailles).

Messiaen Benoît (Belgian) 1994
Utilisation des allèles d'incompatibilité pour l'identification variétale chez l'ananas (engineer thesis, Institut Supérieur Industriel Agronomique de Gembloux).

Müller Agnès (French) 1994
Contribution à l'étude de la fertilité et de l'autofertilité dans le genre *Ananas* (mémoire ISTOM).

Ocampo Pérez John A. (Colombian)

- Morphological and isozyme characterization of papayas from the Antilles and Venezuela (engineer thesis, U. Caldas) 1999-2000
- AFLP characterization of passion fruits (voluntary training, in collaboration with Ray Schnell, USDA-Miami) 2000
- SSR diversity study in papaya (MSc thesis, Ecole Nationale Supérieure d'Agronomie de Montpellier, in collaboration with A.M. Risterucci, CIRAD-AMIS) 2001-2002
- **Etude de la diversité du genre *Passiflora* L. (Passifloraceae) et de sa distribution en Colombie (doctoral thesis, Ecole Nationale Supérieure d'Agronomie de Montpellier, codirection) 2003- 2007.**

John Albeiro Ocampo is now researcher at the Centro Internacional de Agricultura Tropical and Professor at the Universidad Nacional de Colombia

Olaya Arias, Cristián A. (Colombian)
Morphological characterization of lowland passion fruits (2000) and cytogenetic study of Andean passion fruits (2001-2002; engineer theses).
Cristián Olaya was contracted by the Centro Internacional de Agricultura Tropical after he obtained his Engineer diploma. He is still working in the cytology team.

Petersen, Jennifer J. (USA) 2000
Morphological diversity of Passifloraceae subgenus *Tacsonia* in Bolivia and Peru (including training of Patricia Quispe on the Peruvian field collection and Lorena Guzmán on the Bolivian field collection) (undergraduate thesis, University of Oregon).
Jennifer Petersen is now occupying a post-doctoral position at the University of California, Davis, working on crop genetic resources, domestication of tropical fruit trees, and agricultural biodiversity.

Primot, Sophie (French) 2000
Morphological and cytogenetic characterization of three passionfruit species and their hybrids (engineer thesis, Institut National Agronomique - Paris Grignon).
After the obtention of her diploma, Sophie Primot has obtained an expatriate position at the European Commission.

Restrepo Valencia, Maria Teresa (Colombian)

- Morphological characterization of passion fruits (engineer thesis, U. Caldas) 2001
- Morphological characterization and study of cpDNA diversity of papaya and mountain papayas, with PCR-RFLP markers (in preparation for a doctoral thesis, University of Ghent) 2002

Rioux, Vincent (French) 2000
Morphological characterization of Andean passion fruits in Ecuador (graduate thesis, Université d'Angers).
Vincent Rioux has developed his own company in Aubagne (France), producing spirulline and providing support to this production in tropical countries.

Rome, Maxime (French) 2008
Diversity and distribution of the *P. laurifolia* and *P. coccinea* complexes in French Guiana (Msc. thesis, Université de Saint Etienne; year 1).
Maxime Rome has been contracted as curator of the living collections of the Jardin Botanique du Parc de la Tête d'Or (Lyon, France).

Segura Ledesma, Sergio (Mexican)
Distribution et organisation de la diversité des passiflores andines (sous-genre *Tacsonia*) (doctoral thesis, Ecole Nationale Supérieure d'Agronomie de Montpellier, codirection), 1995-2000.
Sergio Segura L. has continued working on fruit genetic resources in Mexico. He is teaching at the Instituto de Horticultura of the Universidad Autónoma Chapingo.

Todou, Gilbert (Cameroonian)
Impact of domestication on distribution and genetic structures of populations of *Dacryodes edulis* (African plum) in Cameroon. (Master thesis, Université de Montpellier,

Doctoral thesis, University of Yaoundé (codirection). 2007-continued
Gilbert Todou is teaching at the Ecole Nationale Supérieure of Maroua (Northern Cameroon).

PUBLICATIONS, COMMUNICATIONS, AND MAIN REPORTS[2]

Articles in refereed journals

Leclerc, C., Coppens d'Eeckenbrugge, G. 2012. Social organization of crop genetic diversity. The G × E × S interaction model. Diversity, 4(1): 1- 32.

Carlier, J.D., Sousa, N.H., Espírito Santo, T., Coppens d'Eeckenbrugge, G., Leitão, J.M. 2012. A genetic map of pineapple (*Ananas comosus* (L.) Merr.) Including SCAR, CAPS, SSR and EST-SSR markers. Molecular Breeding, 29(1): 245-260.

Ocampo, J.A., Coppens d'Eeckenbrugge, G., Jarvis, A. 2010. Distribution of the genus *Passiflora* L. diversity in Colombia and its potential as an indicator for biodiversity management in the coffee growing zone. Diversity, 2(11): 1158-1180.

Bartholomew, D.P., Coppens d'Eeckenbrugge, G., Chen, C.C. 2010. Pineapple. *In*: Clark, J.R. and Finn, C.E. (eds.): Register of new fruit and nut cultivars, HortScience, 45: 740-742.

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Ocampo, J.A., Coppens d'Eeckenbrugge, G., Restrepo, M.T., Jarvis, A. Salazar, M.H., Caetano, C.M. 2007. Diversity of Colombian Passifloraceae: biogeography and an updated list for conservation. Biota Colombiana, 8(1): 1 - 45.

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Article

Social Organization of Crop Genetic Diversity. The G × E × S Interaction Model

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Abstract: A better knowledge of factors organizing crop genetic diversity *in situ* increases the efficiency of diversity analyses and conservation strategies, and requires collaboration between social and biological disciplines. Four areas of anthropology may contribute to our understanding of the impact of social factors on crop diversity: ethnobotany, cultural, cognitive and social anthropology. So far, most collaborative studies have been based on ethnobotanical methods, focusing on farmers' individual motivations and actions, and overlooking the effects of farmer's social organization *per se*. After reviewing common shortcomings in studies on sorghum and maize, this article analyzes how social anthropology, through the analysis of intermarriage, residence and seed inheritance practices, can contribute to studies on crop genetic diversity *in situ*. Crop varieties are thus considered social objects and socially based sampling strategies can be developed. Such an approach is justified because seed exchange is built upon trust and as such seed systems are embedded in a pre-existing social structure and centripetally oriented as a function of farmers' social identity. The strong analogy between farmers' cultural differentiation and crop genetic differentiation, both submitted to the same vertical transmission processes, allows proposing a common methodological framework for social anthropology and crop population genetics, where the classical interaction between genetic and environmental factors, G × E, is replaced by a three-way interaction G × E × S, where "S" stands for the social differentiation factors.

Keywords: crop genetic resources; cultural transmission; *in situ* conservation; interdisciplinary approach; maize; seed exchange; social differentiation; social network; sorghum

1. Introduction

As conservation programs for protected areas and plant genetic resources (PGR) expanded from single species approaches to ecosystem/agrosystem strategies which include the participation of local actors, anthropologists have become increasingly involved in studies and conservation of biodiversity [1]. At the same time, conservation biologists became increasingly aware of the impossibility of maintaining a significant proportion of PGR *ex situ*. Consequently, *in situ* approaches turned out to be essential for preserving agrobiodiversity as well as the underlying processes [2]. In this context, farmers' traditional knowledge has been recognized as a key component of germplasm diversity [3-6]. Thus, both disciplines have had the opportunity to share a common research field and a close collaboration was expected. However, cultural ecology of PGR has mainly focused on the relationship between farmers' behavior and genetic resources, and particularly on farmers' practices and decisions with an effect on genetic selection [1]. As a matter of fact, the contribution of social anthropology has been very limited. Indeed, the social organization of farmers has most often been overlooked as a factor influencing crop genetic organization, and close cooperation between social anthropology and population genetics has remained exceptional. Such a cooperative approach would entail that experts of each discipline develop their methodology in a way that the causes and consequences of observed phenomena can be assessed by experts of the other discipline.

There are several reasons for a limited collaboration. Academically, biological and social sciences remain distinct by promulgating a conception where the "natural" and biological world is opposed to the social and human one [7]. At their interface, social factors are usually reduced to individual choices in the analyses, which constitutes a barrier for social anthropology to step in. The individual based approach is not accidental. It has been the one promoted by the classical western individualistic economic model, which ignores the fact that individuals are part of social networks. This model has been implicitly extended to *in situ* crop genetic studies in conservation biology, where the social component is too often reduced to a sum of individual decisions, motivations and actions. Farmers' networks of relations, which are linguistically and socially structured, have rarely been considered as a factor structuring also *in situ* crop genetic diversity.

The classical economics model, inherited from the seventeenth century, operates with an atomized, *undersocialized* conception of human action referring to a utilitarian tradition. As mentioned by Granovetter [8], the effects of social structure and social relationships on production, distribution, or consumption are weak or inexistent in this model. Individuals do not noticeably influence supply or demand, which are considered as components of the economic system itself. They are anonymous and can be swapped without any effect on economic transactions, which take place without supposing any pre-existing sound social relationships between protagonists. Rather, competition determines the terms of trade, and individual choices are rational by maximizing profitability. Such a conception is favored

by Lacy *et al.* [9] when they hypothesize that sorghum varieties of Malian farmers are a "choice optimizing outputs" in the face of environmental variation.

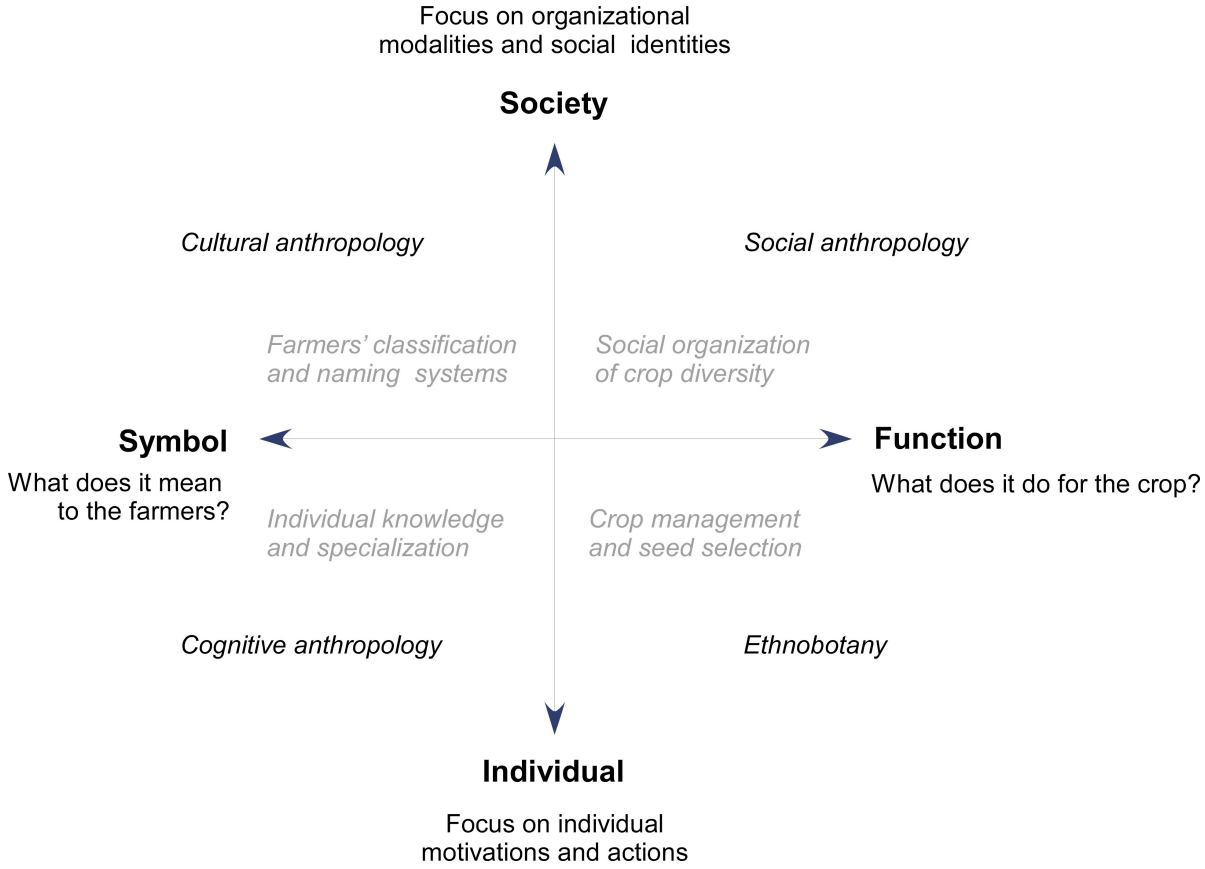
The atomistic view of the individual based approach is familiar in crop population genetics too. Indeed, crop populations are most often considered as an aggregate of individual plants that are interchangeable under the null hypothesis (e.g., permutation test). However, structure is also central in the discipline. Testing homogeneity among populations imposes recognizing factors that could allow their differentiation, through genetic isolation, genetic erosion, and differential selective pressures. A crucial point is that the recognition of populations to be tested, and the factors to be tested, are intrinsically related, and together determine sampling and testing procedures. If a factor is not isolated in the sampling protocol, its effect cannot be measured in terms of population structure.

As for wild plant population studies, sampling strategies adopted for cultivated populations have emphasized "natural" diversification factors, such as geographic distances and barriers, environmental variations with attendant natural selection. Concerning human factors, landrace sampling has placed emphasis on the effects of farmers' practices, selection, both conscious and unconscious, management, and uses, (e.g., culinary preference, agronomic objectives, adaptation to soil and altitude, traditional knowledge) [10]. Implicitly or explicitly, farmers' practices themselves have been associated with particular ethnic groups to explain crop genetic diversity [11] and justify *in situ* conservation.

The present article analyzes why an individual based approach is limiting in crop genetic studies and how social anthropology can contribute to correct this situation, with its classical framework for social organization, cultural transmission and differentiation processes. Observing that the transmission of seeds and the associated knowledge are affected by marriage and residence rules through inheritance and exchange, it describes how social factors organize crop genetic diversity *in situ*. Considering domesticated genetic resources as social objects, it proposes an integrative approach that can be used to design sampling strategies for different levels of sociological integration.

Figure 1 presents studies on the social component of crop genetic diversity in a diagram based on a double contrast. While farmers can be studied individually (as actors), or socially (comparative sociology and economy), the effect of the social component can be tackled from a functional perspective ("what does it do to the crop?") or a symbolical perspective ("what does it mean for the farmer?"). The left side of the diagram includes the traditional fields of cognitive (lower left) and cultural (upper left) anthropology, while the right side encompasses the traditional fields of social anthropology (upper right) and ethnobotany (lower right). In the horizontal axis, the symbolical perspective considers farmers' world perception, including folk taxonomy (bearing on humans, plants, animals, and environment), whereas the functional perspective places emphasis on what the observer can deduce on farmers' practices referring to his/her own perception or theoretical background—e.g., functional analyses in ecology [12,13]. The vertical axis presents the contrast between individual based approaches, where emphasis is placed on farmer management and practices, and social based approaches, which emphasize social organization of farmers. In the latter case, the contribution of social anthropology is essential in considering rules that organize marriage, post marital residence, filiation, inheritance, and determine residential or linguistic endogamy. The fact that these rules organize exchanges within and among groups, including seed movements, justifies the specific contribution of social anthropology in the study of crop diversity.

Figure 1. Diagrammatic representation of the main fields of anthropology that study the social factors affecting crop diversity, with examples of specific areas (in grey), according to the focus on functional *vs.* symbolical analysis, using either individual or social based approaches.



Thus, Figure 1 situates this contribution of social anthropology when combined with crop population studies as compared to classic ethnobotanical approaches. Crop genetic diversity studies mostly belong to the right half although cognitive and cultural aspects have functional consequences on crop management. Most field studies fall in the lower right quarter, as they focus on functional analyses of individual farmers' practices and knowledge, attempting to deduce mechanisms of crop genetic diversification and measuring their relative effects at the field, farm, or village scale. Their protocols combine ethnobotanical methods and genetic analyses. Individuals can be further grouped into *a priori* categories (by gender, age, access to the market, economic status), or a typology resulting from multivariate analysis [14-18].

As far as PGR are concerned, the upper right quadrant has been much less explored. Indeed, few studies have used a social based approach with a sampling strategy addressing the effect of social organization on crop genetic diversity *in situ*, at different levels of social and geographical integration. Zimmerer [19] studied seed movements of potato and ulluco in the Peruvian Andes and showed how social and environmental factors can produce a multilevel geography of seed networks and seed uses. van Etten [20-22] followed a similar approach for maize in Mayan communities of Guatemala, adding an historical perspective to explain the observed geographic pattern of maize genetic diversity. Inspired by Granovetter's approach and emphasizing social embeddedness of transactions,

Badstue [23] considered seed exchanges under an economic perspective, focusing on the dynamics of maize diversity (conservation) and the introduction of improved varieties (innovation). She based her social approach on the concepts of social network, social capital, involving trust in seed transactions, and collective action. Perales *et al.* [24] and Brush and Perales [25] have tested the effects of cultural contrasts on crop management and resulting genetic differentiation. Here we propose to extend this approach and use the tools of social anthropology, involving residential and kinship organization [26], to investigate the effect of social factors on the dynamics of crop genetic diversity.

Can social embeddedness of seed exchanges improve our theoretical and empirical approach of *in situ* crop genetic diversity? Do farmers' social and linguistic identity as well as correlative social differentiation processes shape *in situ* crop genetic diversity by compartmentalizing seed exchange systems and limiting seed-mediated gene flow? Based on a review of maize and sorghum studies, and embracing a social anthropological approach, this article aims at showing that *in situ* crop genetic diversity *cannot* be fully understood without taking into account the social organization and the cultural identity of farmers. Following Granovetter's network methodology, our hypothesis considers that farmers' purposive actions are instead embedded in concrete, ongoing systems of social relations. Farmers are neither anonymous nor interchangeable as they are members of groups where persons have to trust each other when exchanging information and seeds that are so important for their subsistence [23].

Section 2 reviews *in situ* crop genetic studies. It focuses on the two most extensively studied cereal models, namely sorghum and maize, pointing out to the shortcomings of the G × E approach (G and E representing respectively genetic and environmental sources of variation) at different levels of spatial integration. Section 3 presents the basis of Granovetter's social network methodology and the anthropologist's concepts of cultural diversity. Human cultural identities result from historical processes implying social barriers, which do not necessarily involve isolation by distance. In consequence, crop diversity studies taking into account social identity of farmers may not fit well into the most common metapopulation models and more specific models are needed [27]. The explanatory models used in social anthropology for the organizational modalities of human societies and cultural diversity are presented, and their interest for crop genetic diversity studies is discussed. In the third section, crop varieties are considered as social objects, inherited and exchanged in the same way as other cultural traits (*i.e.*, rules for marriage, postmarital residential group, filiation, *etc*.). Many examples illustrate that traditional knowledge as well as seed exchange systems are embedded into social structure, favoring vertical transmission of both knowledge and PGR through a centripetal system. The overall discussion focuses on the social based approach that allows us to consider crop diversity organization as resulting not only from an interaction between genetic and environmental factors, G × E, but from a three-way interaction G × E × S, where "S" stands for the social differentiation factors. Implications for *in situ* sampling strategy and participatory plant breeding are worked out.

These G × E and G × E × S expressions are inspired from the usual practice of analysis of variance for variety trials. Basic analyses of population genetics work in the same way, comparing components of variation in crop populations at different levels. Whether considering quantitative traits variation or genetic diversity, the common point is that any particular factor must be specifically represented in the data structure to be correctly analyzed and interpreted. Thus, the G × E × S expression highlights

the need to consider farmers' social organization as a specific factor in the collection of data and their analysis.

2. Overview of *in situ* Crop Genetic Diversity Studies

Among studies on *in situ* crop genetic diversity, the two most explored crop models are sorghum in Africa and maize in Mesoamerica. A number of studies have attempted to establish a link between farmers' management (involving folk classification, exchange and selection of seed) and the organization of genetic diversity as observed at different spatial scales (continental, national, regional and local). However, as far as we know, no published study has clearly taken into account the effect of farmers' social organization on crop genetic resources. So far, geographic and social factors have not been analyzed separately, and reference studies have mostly followed a G × E approach, where the effects of social organization have been blurred.

2.1. Sorghum Studies

Sorghum (*Sorghum bicolor* ssp. *bicolor*) is a major cereal, domesticated in Africa about 8,000 years ago [28], widely cultivated in the semi-arid tropics and the warm temperate regions of Africa, Asia, and America as a staple, fodder, and/or for the preparation of beer and syrup. Sorghum is wind-pollinated and predominantly autogamous. However, outcrossing is not negligible, with rates ranging from 5 to 40%, as estimated from biochemical and molecular markers [29-31].

The infraspecific classification of *Sorghum bicolor*, by Harlan and de Wet [32] and de Wet [33], recognizes three subspecies, subdivided into races. The concept of "race" was defined first by Anderson and Cutler [34] to classify morphological maize diversity as "a group of related individuals with enough characteristics in common to permit their recognition as a group". It constitutes for both sorghum [35] and maize [25] the unit of analysis of *in situ* crop diversity (although it is not a valid level of plant taxonomy). No interfertility barriers have been reported between sorghum infraspecific categories.

Sorghum bicolor ssp. *bicolor* regroups domesticated grain sorghums, including their five basic races (bicolor, guinea, caudatum, durra and kafir), with particular, although overlapping, geographic ranges, and ten hybrid races that combine characteristics of at least two of these basic races [32]. The morphological distinction of grain sorghum races is essentially based on spikelet morphology, correlated to panicle shape, and their unity would be related to the ethno-geography of the peoples who cultivated sorghum, as first proposed by de Wet and Huckabay [36].

Thus sorghum represents a rare case where the importance of social factors on genetic diversity is recognized in the foundation of a scientific classification. As stated by de Wet [33] "racial evolution of grain sorghums is closely associated with ethnological, ecological and geographical isolation. Variation within races is determined by conscious selection for particular uses, and to satisfy the individual fancies of cultivators" [33]. For example, according to Stemler *et al.* [37] and Harlan and Stemler [38], the race caudatum was associated with the speakers of the Chari-Nile languages in Africa and the race kafir was derived from early bicolor of northern Africa and carried south, primarily by Bantu speakers. In this picture, two social factors, differential selection and restricted seed exchanges

between ethnic or linguistic groups appear to have played an essential role in shaping the current morphological differentiation of sorghum races.

2.1.1. Sorghum Diversity at the Continental Scale

The hypothesis of de Wet and Huckabay [36], where the differentiation of African farmer languages is presented as a factor having shaped sorghum diversity across Africa, has never been tested, even though it has been mentioned by many authors [33,37-39]. Indeed, most studies at the continental scale have used the racial classification of Harlan and de Wet [32] as an interpretation grid, "race" being treated as a biological factor. Several studies have tested the consistency of this classification with morphological [40,41], biochemical [42] and molecular markers [43-48]. The racial classification was partly validated by morphological analyses, whereas biochemical and molecular markers have situated most of the genetic variation at the accession level, giving relatively little importance to races or the race × origin interaction in the organization of genetic diversity. The social identity of farmers was never taken into account in the sampling strategy, but considered as a discussion point supporting *a posteriori* the interpretation of data. For instance, from their RFLP study, Deu *et al.* [45] concluded that "the neighbour-joining analysis suggests two major geographic poles for sorghum evolution (…), [agreeing] with indications of ethnic divisions between northern (Nilotic and Sudanian languages) and southern Equatorial Africa (Bantu languages)".

2.1.2. Sorghum Diversity at the National Scale

Despite the wide geographic range covered by national studies (Ethiopia, Eritrea, Sudan, Benin, Burkina Faso, Niger, Morocco, India), most of them, based on an essentially G × E approach, have produced strikingly similar pictures. "Regions" were only defined in geographical terms, and not characterized sociologically. Sampling was sometimes limited and/or done through *ex situ* collections [48,49], so the social identity could not be tested. In those studies using direct field sampling, few fields were selected in each region or locality. For instance, Djè *et al.* [50] and Medraoui *et al.* [51] used a hierarchical sampling design with five "regions" and four provinces, respectively, from north-western Morocco. Djè *et al.* [50] selected four fields within each region and, in each one, 15 inflorescences from randomly harvested individuals. The sampling strategy of Medraoui *et al.* [51] involved an average of 2.4 localities per province and 12 individuals per locality. Kayode *et al.* [52] used 72 "farmers' varieties" randomly sampled (the number of farmers is not specified).

These studies show divergent patterns of geographical/environmental distribution for morphological and genetic diversity. Morphological diversity is mostly found among regions or distant fields [53-56]. Environmental adaptation is mostly observed through quantitative variation, affecting very few qualitative traits such as panicle compactness and shape [53,57,58]. By contrast, biochemical and genetic diversity is found essentially at the local level, and even at the field level [30,50-52,55,57-60]; its organization shows no environmental component, even when the geographic range of the studies include sharp altitudinal or precipitation gradients [29,48,61].

In most of these studies, the weak contribution of geographic distance to the organization of genetic diversity has been attributed to open and extensive seed exchanges among farmers, a fact which has not been verified in a systematic way. Furthermore, this interpretation is difficult to reconcile with

observations on the structure of morphological diversity at the regional and local levels. How can gene flow be significant at the region or country level, but not at the local scale or even field level, where it is much more likely? The contradiction is particularly visible in the successive studies of Djè *et al.* [30,50,55,56], who explained the wide morphological variation across fields and regions by limited seed exchanges and divergent selection practices among farmers, while their biochemical/molecular results led them to conclude on widespread seed exchanges, and to consider morphological differentiation as the direct effect of farmers' selection.

Widespread seed exchanges at the national level is further contradicted by the only study integrating an explicit ethnic component, carried out in Niger by Deu *et al.* [62]. This survey is also the most extensive national study, bearing on 484 accessions from 79 villages and taking into account environmental, ethnic as well as sorghum racial data. In each village, all local varieties listed by a representative group of farmers were sampled. The superposition of geographical and ethnic patterns causes "strong geographical × ethno-cultural interactions in the structure of crop genetic diversity" entailing a difficulty to distinguish between these factors. In any case, genetic differentiation was much lower between rainfall zones than between geographical regions × ethnic groups, indicating that historical patterns prevailed upon environmental conditions. Furthermore, a spatial correlation of genetic diversity was detected within 100 km, even after correcting for the "racial" component of sorghum organization, pointing to restricted seed exchanges among farmers, even within ethnic groups.

The few studies of sorghum genetic diversity carried out at the local level have focused on the fields, landraces, farmers' practices, and individual characteristics of farmers living in a same village (e.g., [14,15]), and have not addressed the effects of social structure on the organization of sorghum genetic diversity.

2.2. Maize Studies

2.2.1. Maize Diversity at the Continental Scale

Maize (*Zea mays* ssp. *mays*) is intimately related to Native American societies, and more particularly to the Mesoamerican cultural area. Archaeological, glottochronological and genetic data consistently point to a very ancient domestication of maize, 7,000 to 10,000 years ago, in Mexico [63-65]. The crop soon started to diffuse both northward and southward, around 4,000–3,000 BP, according to available macrobotanical remains [66,67], or much earlier (8,000 BP), according to microbotanical remains [66]. The earliest macrobotanical remains in southern South America are dated *ca.* 2,000 BP. Genetic studies of modern maize races indicate a progressive expansion of maize, with subsequent isolation by distance and a concomitant loss of diversity; the high correlation between geographical and genetic distances shows a strong geographical component in the organization of genetic diversity at the continental scale [68]. Genetic variation among races is limited to 7–8% of the total [68].

The very ancient history of maize cultivation has resulted in an impressive morphological and phenological diversity. In a first modern effort of classification, based on morphological as well as on genetic, cytological, agronomic characteristics and the geographical distribution, Wellhausen *et al.* [69] recognized 25 Mexican races, classified in four main racial groups, plus seven unclassified morphotypes that would have arisen through hybridization. The racial classification was extended and

systemized to more germplasm in Mexico as well as many other countries, using the methods of numerical taxonomy. This approach has been enriched with biochemical markers (isozymes, kernel components, secondary metabolites) and molecular markers, which were most useful in describing new races (for a total of 59 to 75 for Mexico) and their relations and in identifying racial complexes [70].

There are consistent indications of social factors affecting maize racial diversity. Hernández and Alanís [71] identified a link between a northern Mexican racial complex and the races from the southwestern USA, suggesting that the latter diversified as a result of northward migrations, through consequent geographic isolation and new selective pressures, related to new environments or new culinary and religious uses. Similarly, the isozyme analysis of the southwestern USA maize demonstrates "a correlation between the cultural-linguistic identity of the Indian tribes and the corn that they grow" [72]. Benz [73] observed an association between a dozen races and farmers speaking Otomanguean languages, this geographic coincidence indicating that both human linguistic and maize racial differentiation have resulted from closely related human cultural and crop biological histories. Going further along this line in an attempt to reconstruct the evolution of the crop from 7,000 to 2,500 BP, Bird [74] defined six maize-cultural regions by comparing the geographic distribution of races and racial complexes of maize to those of cultural traits of past civilizations at a continental scale.

2.2.2. Maize Diversity at Regional Scales

As a biological model, maize mostly differs from sorghum in its clearly allogamous breeding system. However, there are many common aspects between the two cereals, and most subregional diversity studies have produced strikingly similar results. Indeed, farmers are reported to exchange a small but not negligible proportion of their seeds, and they sow several landraces in a same field, allowing for frequent cross-pollination. As in sorghum, the weak regional organization of maize neutral genetic diversity, considered by most authors as the result of an open seed system, contrasts with a marked morphological differentiation [5,24,75-79]. Some of the variation in quantitative traits is attributed to environmental adaptation, particularly in relation to altitude, but most morphological differentiation has been attributed to the phenotypic selection exerted by farmers. As in sorghum, seed lots are very limited in size (1–2% of the harvested ears being used for seed), and selection is mostly exerted on characteristics of harvested ears and their kernels, but other traits are genetically associated [5,80,81]. Therefore, the maintenance of landraces should imply a considerable level of consensus both among and within the communities exchanging their seeds. In fact, the ideotypes shaping the outcome of maize selection vary among ethnolinguistic groups [24,79].

Brush and Perales [25] tested the effect of social origin of farmers on maize population across Chiapas landscapes, comparing practices of *mestizos*, Spanish speaking people who identify to the Mexican national culture, and indigenous people, primarily speakers of one of several Mayan languages. They put forward the recurrent differences between the two groups concerning the economic orientation (commercial *vs.* subsistence), races of maize grown, predominance of local *vs.* improved varieties, age of seed lots, seed color, as well as the seed exchange systems. Seed exchanges are more within-community oriented for indigenous people than for *mestizos*. Bellon and Brush [80] suggested that maize diversity is also influenced by social organization, notably land fragmentation, and the *ejido* rule favoring non-partible inheritance of land and prohibition against selling and renting

lands. These case studies point out the importance of the social context, as many practices can be interpreted in terms of cultural attributes of the considered social groups affecting crop diversity.

Despite the relative consensus of most research teams, the picture of maize diversity mostly driven by small but significant seed exchange in traditional systems may still look unsatisfactory on several aspects. Thus, a professional breeder might be surprised by the presumed efficiency of mass selection, focused on a few traits, maintaining phenotypically and phenologically well differentiated landraces of an outcrossing crop in an open system (while seed companies have to grow and screen several generations to breed a new cultivar, to be propagated under highly controlled isolation). In addition, as for sorghum, if seed exchange exists at the regional scale, the reason why genetic differentiation is higher at the local scale [77] than at the regional level remains unclear.

Interestingly, a few studies have challenged the model of open maize genetic system. Dyer and Taylor [82] underlined that case studies have often been incomplete and biased because they were designed to explain maize diversity on individual farms, neglecting farmers' practices after introduction, seed demography across farms and its diffusion through seed systems. For example, most introduced seed is replaced after its first year, at about twice the rate for local seed. According to their country-level dataset for Mexico and their demographic model, seed diffusion varies widely, with 1% of lots multiplied 10-fold in 5 years and 60% not diffusing at all. Exchange rates reported for Cuzalapa [75] are usual for western Mexico, but up to 10 times higher than in other localities. Saved seed acquired locally diffuses more than expected, while new introduced seed does not diffuse so much. Dyer and Taylor highlight that maize diversity is maintained at the locality level, not at the farm level, the former being the unintended result of individual farmers' actions.

Van Etten [21] underlined that studies on regional distribution of maize diversity had not taken into account geography and history, while archaeology suggested radically different spatial distributions in pre-Columbian and early colonial times. His revision of the central Guatemalan history led him to the hypothesis that seed dynamics might have followed regional interactions, concentrated in catastrophic events and massive migrations, and trade relations, embedded in a political economy that is narrow in its geographical scope, because it necessarily reflects the ties between communities. By contrast, most daily social interactions were very local in scope, allowing for the development of maize diversity under geographic isolation. Van Etten *et al.* [20] tested part of these hypotheses in 13 localities from four townships of Chimaltenango (Guatemala), using SSR (single sequence repeats) markers and morphological characterization. It is interesting to note that people in these townships speak different dialects of a same language [83]. Cluster analysis of SSR data showed a clear spatial genetic structure, as clusters mostly corresponded to localities and were further associated by township. In two cases, similar germplasm was found in different townships, indicating some regional seed exchange. A high isotropic spatial autocorrelation indicated isolation by small distances within localities (less than 8 km), probably caused by a much higher exchange rate among close neighbors (let us note the similarity with Bellon *et al.* [84] study reporting 92% of seed lot exchanges within 10 km in Mexico). At a wider scale, between townships, geographical distance does no longer constitute the main factor, and seed movements have followed another logic, combining environmental (altitude) and/or historical constraints, as well as relations with traders (centrality of provincial market, consumer acceptance, *etc*.). According to Van Etten *et al.* [20] low regional genetic differentiation, as found by his group in

Guatemala and by the other teams in Mexico, does not imply currently high levels of gene flow, and could be explained by intensive gene flow in the past. This argument is similar to the interpretation of Deu *et al.* [62] about the historical determinants of the distribution of sorghum genetic diversity in Niger.

3. Farmer Social Organization and Cultural Diversity

Our review of the sorghum and maize cases shows that most agrobiodiversity studies have placed emphasis on the environment and reproductive biology as organizing factors, social factors being considered as a particular component of the crops' general environment. Indeed, they were most often restricted to farmer practices, whose impact on the crop can readily be integrated in an individual based approach (falling in the lower right quarter of Figure 1). As such, the cultural identity of farmers, including their social organization (upper right quarter of the figure), and its interaction with crop genetic diversity have remained understudied. Before discussing this interaction, we shall recapitulate Granovetter's views on economic transactions and summarize basic explanatory models used in social anthropology to explain cultural diversity.

3.1. Social Embeddedness and the Orientation of Exchanges

Many studies on social networks show that individual behaviors cannot be analyzed without referring to the concrete network of social relations. A parallel can be drawn with the approach promoted since the 1970's in economics by Granovetter. Following the development of the economic anthropology after Polanyi [85], he has changed the way of thinking about the modern economy by focusing analyses not on individuals, but on *relations*, thus calling into question the premises of the classical theory according to which transactions result from rational choices of individuals considered as independent. Instead, Granovetter shows that, in modern societies, economy is embedded into social relations that are to be considered in the analyses of exchanges. In fact, economy is not a separate domain of sociology.

As mentioned by Laville [86], embeddedness is observed at two levels: the first one, interpersonal, refers to the concrete relations between individuals, and the second one, structural, depends on the characteristics of the network itself, which can be coupled or decoupled [87]. A *coupled network* is one where all individuals are linked to all others by many relations, and a *decoupled network* is one where two or more primary networks are linked together by weak ties. Presence of weak ties between primary networks favors the diffusion of information. Granovetter [88] points out the "strength of weak ties" resulting from their role as a "bridge" between primary networks. Conversely, the absence of bridges between two primary networks means that they are strictly decoupled and that the information available in the first one cannot diffuse to the second. In such a case, the exchange system is necessarily within-group oriented.

Such a methodological approach fits quite well with the anthropological analyses of social differentiation that imply decoupled networks. A good illustration is that of the linguistic differentiation of human communities, supposing that spatial isolation or social barriers are maintained over generations. Besides, other organizational modalities of human communities, described by social anthropology, may also impact the orientation of the exchange systems.

3.2. The Anthropologist's Concepts of Cultural Diversity

Social organization refers to the internal differentiation of human society, considering that society is not a homogenous mass or a simple collection of individuals. Many levels of sociological integration can be considered here: family, lineage, village or residential group, tribe, sub-tribe, linguistic groups. These levels correspond to different sets of cultural traits. The membership to a social unit can be inherited (descent groups) or result from recruitment (e.g., professional activities).

The correlative concept of social identity is a means of categorizing oneself and others in an organizational sense. As stated by Longley [89], "the we/them dichotomy is based upon the implicit or explicit contrasts between one's own group and that of others", implying the maintenance of boundaries through social processes of exclusion and incorporation [90]. As a social group is more than the sum of its individual members, its characterization cannot be based on that of individual behaviors and choices. Organizational modalities of collective life have been usually described through affiliation, residence, and marriage rules. Functionally combined, these rules support the social identity of human groups.

3.2.1. Organizational Modalities of Human Societies

The anthropological concept of consanguinity refers to members that are true or putative descendants from a common ancestor. Affiliation can be patrilineal (common in African, Circum-Mediterranean, and East Eurasian societies), matrilineal (Insular Pacific and North America) or a combination of both (America) [91]. The anthropological concept of consanguinity cannot be assimilated to the biological concept of consanguinity. It is a cultural attribute defining the membership to the lineage or clan. The impact of the differentiation process through affiliation on human collective life is further strengthened by marriage rules. Indeed, lineage exogamy implies that a member of one lineage cannot marry another member of the same lineage. Thus, lineage affiliation practically divides the human's world in two fundamental categories: the one where he/she cannot find a mate (same lineage) and the second where he/she can (different lineage). A third organizational modality of collective life is the postmarital residence or transfer of residence of man or woman. The most common form is patrilocal residence, where the woman comes to live at the husband's location.

The composition of the residential group is determined by the combination of affiliation, marriage and post marital residence rules. Obviously, spatial distribution of differentiated groups is an integral part of the social process. It is common that members from a same lineage are distributed in multiple residential groups and can get marriage within (residential endogamy) or out of their own residential group (residential exogamy). The residential endogamy rate indicates how open (or closed) is the between-groups social relation network, but this rate must be related to the considered social/spatial scale. Indeed, the endogamy rate may increase with the level considered (residential group, tribe, or linguistic group). The maximal endogamy rate indicates the level of sociological integration where the process of exclusion and incorporation maximizes centripetal relations and exchanges through marriage.

The basic assumption underlying cross-cultural research is that "the elements of any culture tend over time to become functionally integrated or reciprocally adjusted to one other" [91]. Functional analyses focus on combined organizational modalities, for instance, correlating marital residence to the

female contribution to subsistence [92], or studying the social evolution from matrilineal cultures that become patrilineal when they acquire cattle [93].

Data sets including cultural traits allow phylogenetic approaches that are similar to those used in biology even though the rhythms and modalities in the transmission of cultural and biological traits are not the same [94,95]. The analogy also concerns linguistic differentiation as an isolation process, linguistic divergence occurring after speech communities have divided "in a similar process to speciation among isolated biological populations" [96,97]. Geographic isolation is a powerful driver of linguistic differentiation, as exemplified by the evolution of Austronesian languages, spoken in islands. On the other hand, it cannot explain that of bantu languages that "are spoken across the continental land mass of sub-Saharan Africa" [96]. Indeed, among the 6,809 languages around the world, 2,058 (30%) are spoken in Africa [98], including Bantu languages. In this latter case, as highlighted by Holden [96], "social factors rather than geographical barriers must have maintained distinct speech communities". Thus, the island explanatory model is not sufficient to explain cultural and linguistic diversity, just as it is insufficient to explain crop genetic diversity.

3.2.2. Cultural Diversity Explanatory Models

Cultural diversity is closely related to mechanisms of cultural transmission, which refer to the process of social reproduction in which a culture's technology, knowledge, behavior, language, and beliefs are communicated and acquired [94]. Hewlett *et al.* [99] revised the three basic models developed to explain cultural diversity. The *cultural diffusion model* assumes that cultural traits diffuse between groups (horizontal transmission). Social groups in closer geographic proximity will share more cultural traits because they should interact more regularly. In this case, the social distance should be correlated with geographical distance. In contrast, the *demic diffusion model* emphasizes the vertical transmission of cultural traits ("semes" in Hewlett's terminology), based on parent-to-child transmission, and strengthened by the trait frequency in the group [94]. According to this model, which appears very similar to genetic transmission, cultural traits diffuse together with group members. Thus, they tend to be reproduced within the group over generations, favoring social differentiation. This conservative model should be crucial in crop genetic studies considering crop varieties as cultural objects. The third one is the *local adaptation model*, or cultural ecology theory of Steward [100], hypothesizing a correlation between environmental conditions, technology and social organization. Accordingly, social differentiation cannot be explained in this model without considering environmental constraints and technical systems.

In a combined analysis of 42 cultural traits, genetic (26 loci), linguistic and geographic distance data from 36 African ethnic groups, Hewlett *et al.* (2002) showed that demic diffusion explains the transmission of 20 cultural traits, especially those related to kinship, family and organizational modalities of collective life, and shifting cultivation. These traits are very conservative by comparison with others and their distribution is "due to expansion of particular people rather than cultural diffusion or local adaptation". Cultural diffusion explains the distribution of 12 semes related to house construction and postpartum sex taboos. Only four semes are linked to local adaptation, and they appear to be variations of demically transmitted traits [99]. The clear dominance of vertical transmission over the two other models is also expressed in the general convergence between human

genetic distances, linguistic distances, and cultural distances. As stated by Hewlett *et al*. [99], cultural traits and genes coincide "because both are affected by the conservatism of vertical transmission".

Thus we propose to consider domesticated genetic resources as social objects, whose transmission is governed by a combination of social and biological processes. As a working hypothesis, we state that if seeds circulation is affected by marriage and residence rules, then they are submitted to the same vertical transmission processes that govern social reproduction. The resulting genetic structure of crop genetic resources will depend on the interactions between this social process (defining rules of residence and transmission involving seed exchanges) and the biological processes of local adaptation and spontaneous genetic exchange, mostly through pollen-mediated gene flow. Verticality in genetic transmission will be associated with seed saving, within-group-oriented seed exchanges (influenced by the rate of residential endogamy), clonal reproduction, and plant autogamy, whereas horizontality will be associated with among-groups seed exchanges (residential exogamy, local and national seed markets), plant allogamy and wide pollen dispersal. In this view, social and biological factors must be considered simultaneously and at the same level in the analyses, using a common theoretical and methodological multidisciplinary framework.

4. Mechanisms Leading to Social Organization of Crop Genetic Diversity

Among the drivers of crop genetic differentiation, only mutation can be overlooked as far as the interaction of social and biological factors is concerned. Genetic drift is affected indirectly, through the size of the plant (sub) populations managed at different stages of cultivation, while selection and migration are likely to be directly affected by the organization of agricultural societies. Selection will be affected mostly through crop management and uses, therefore it will depend on the distribution of knowledge, practices and preferences among and within human groups. Migration will be affected by any barrier to seed exchanges related to social differentiation. Human effects on both selection and migration must be considered at all levels of sociological integration.

4.1. Traditional Knowledge, Perception of Crop Diversity and Conservative Selection

Analyses of ethnobotanical knowledge reveal the dominance of vertical transmission. Thus, comparing vertical, horizontal and oblique transmission, Reyes- García *et al.* [101] found no evidence of horizontal transmission of ethnobotanical knowledge in the Tsimane from Amazonia. Lozada *et al.* [102] underlined the role of the family in a rural community of Patagonia, demonstrating the essentially vertical transmission of wild plant knowledge, while Ohmagari *et al.* [103] estimated that 80% of indigenous knowledge of Cree communities (93 items or skills were analyzed) are acquired from parents and grandparents.

Hewlett and Cavalli-Sforza [104] present a remarkable study on foraging techniques among Aka Pygmies, associated with Bokola villagers who live in the same section of the village. This situation provides a favorable context to illustrate the verticality of knowledge transmission and the mechanisms of ethnic isolation. Analyzing the cultural transmission of 50 foraging skills among 72 Aka individuals, Hewlett and Cavalli-Sforza [104] showed that vertical (parent to child) transmission is by far the most important mechanism, accounting for 86.9% of the cases studied. Correlatively, Bokola villagers are poor contributors in this transmission (1.6%). Thus, despite the close geographic

proximity allowing for daily interactions between Aka and Bokola, the latter do not contribute significantly to the Aka knowledge. The verticality of the knowledge transmission favors the cultural differentiation between the two groups, as stated by Cavalli-Sforza and Feldman [94]. The cultural transmission concerning crop diversity should follow the same mechanisms, as agriculture and seed selection are family domains.

Intercultural comparisons on perception of crop genetic diversity are difficult and very few studies have addressed this subject at this level. In their analysis of 16 species among 29 communities in eight countries, Jarvis *et al.* [105] observed great differences among communities from the same country. For a better comparison, we have selected from their data pairs of communities settled in similar environments. Thus, in the Amazon lowlands of Peru, farmers from the Aguaytia valley manage intraspecific cassava variability with 39 named categories while their neighbors of the Pichis-Pachitea valley, distant of 80 km, use twice this number, with 89 categories. Similarly, in the Ethiopian highlands, the Ankober manage five categories for barley, while the Tarmaber manage 12, only 52 km further. In Burkina Faso, the Pobe, as compared to the Tougouri distant of 207 km, manage twice the number of categories for pearl millet (18 *vs.* 9) as well as for sorghum (27 *vs.* 15). In Mexico, the Yaxcaba and Ichmul distant of only 47 km, manage similar numbers of categories for beans (7 and 8 respectively), chili (4 and 5) and squash (3), but not for maize (14 and 9). Such figures not only point to the contribution of cognitive and cultural processes in crop diversity distribution or classification, but also to the fact that, conversely, this distribution reflects social differentiation between communities (but see potential effect of economic orientation [25]).

If the biological potential for differentiation is roughly constant within a given crop species, understanding the operation of farmer classification becomes essential to interpret variation among nomenclatural and classification systems used for on-farm management. An intercultural comparison of crop genetic diversity obliges us to adopt a new interdisciplinary approach. Biological variability, indeed, is usually considered as a cause and the number of categories (or farmer-named varieties) as a result. However, if farmer crop selection is based on prerequisite "mental images" with a particular place in the classification system, the cultural process appears to be first and the biological existence of the distinguished morphotypes a result. In other words, farmer categories have to exist in farmers' minds before they exist in their fields. In any case, there is necessarily a cultural consensus [106] on crop classification to ensure both the transmission of knowledge over generations and the communication between farmers.

Studies on farmers' traditional agricultural knowledge or on their ability to distinguish and to name varieties have been mainly carried out at the village level within a same linguistic group, emphasizing on individual-level variations ([107], for an overview). James Boster, a pioneer in this domain, has shown how the cognitive aspect is influencing crop selection with reference to the intraspecific classification system: "crops show the effect of the cultivator's eye as well as hand. […] perceptual distinctiveness is a necessary condition for cultivar maintenance; cultivars must be distinguishable before they can be selected…" [108]. Thus, the "mental image" of the variety is just as necessary for farmer selection as is the *ideotype* for professional breeding. Moreover, perceptual distinctiveness and classification systems also constitue a key component of the adoption process. Selection and adoption proceed similarly. Identification based on an existing categorization is needed to apply selection and a "new" variety is considered as such and adopted only if it can be distinguished from already known

varieties. In both cases, the cultural intraspecific classification system works as a conceptual frame of reference through identification (to select the same) or distinction (to adopt the new). In Cuzalapa (Mexico), farmers' seed selection practices essentially aim at maintaining the phenotypic integrity of their traditional maize cultivars [81]. In a more precise study, Benz *et al.* [79] have shown how Tzeltal and Tzotzil farmers maintain separate maize populations through perceptual distinctiveness, each ethno-linguistic group being able to recognize its own landraces from those of the other group. In Guyana, Elias *et al.* [17] described how the Makushi care for spontaneous cassava seedlings, select and assign them to their previous categories. Those seedlings that are too distinct from existing varieties do not receive specific new names. Duputié *et al.* [109] reported a similar practice among the Wayãmpi of French Guiana, and showed that off-type phenotypes are counter-selected in subsequent vegetative cycles.

When managing to reproduce its categories at each cultivation cycle, first selecting the seed genitors, the farmer is confronted to the contradiction between the biological continuum of individual variation and the radical discontinuity of her/his cultural classification. This contradiction depends partly on the plant reproduction system. Indeed, in their wide comparison of nomenclature systems across species, cultures, and countries, Jarvis *et al.* [105] show that farmers use more detailed classifications for clonally reproduced crops (33.4 terms) than for inbreeders (12.8 terms), partial outbreeders (10.9 terms) or outbreeders (9.3 terms).

Many anthropologists, following Berlin's work [110-112], have compared folk classification, internal to the studied society, with the western scientific nomenclature as an external reference. Others, like Martin [113], have argued against such analyses, underlining the incongruity of the comparison, which finally consists in detecting in folk classifications the hierarchical, Linnean or varietal, system developed in western cultures. Indeed, the reference to an external system, used in a very different social and cultural context (where scientists themselves should be considered as a social group), neglects the essential link of the folk classification to the group involved, *i.e.*, the fact that the objects only exist as such because they take a place into a culturally defined system of oppositions, which makes sense to the group. Thus, a much more meaningful approach would pay attention to the coherence of the classificatory series inside a society itself by paying equal attention to their use in different domains (which leads us to the upper left quadrant of Figure 1), for example by relating the identity of crop categories to the social classification of the farmers themselves. A common case is when landraces from other groups are recognized and named as such. Thus, Mexican farmer communities distinguish their maize landraces from those of other communities, calling their germplasm as "our maize", and they maintain its morphological distinctiveness [24,79]. In some cases, farmers may consider differences in the reproduction process, even though they do not translate into genetic, morphological or agronomical differences. Keralan Farmers (southern India) perceive, name, evaluate and manage distinctively coconut hybrids that are genetically and morphologically identical. They value better those spontaneous hybrids that they identify in their fields, than those obtained through technically controlled pollinations in experimental stations [114]. Haudricourt [115] provides an even more striking example where he describes a parallel between the social classification of a New Caledonian society into patrilineal clans and the categorization of yam clones. With 72 categories, there are as many clones of yam as there are clans. At the rite of enthronement of the leader of a new

clan, a new clone is taken from the fallows. The sexual reproduction guarantees the originality of this material associated to the new clan.

This brief analysis of the relationship between social differentiation, cultural transmission, and perception of crop diversity, with consequences on the processes of selection and adaptation of biological materials, shows that the cultural process is causal in shaping intraspecific morphological diversity. Accordingly, cultural and linguistic surveys have to precede the definition of the strategy for crop germplasm sampling.

4.2. Seed Exchange Embedded into the Social System and Vertical Transmission

If crop categories are social objects, their transmission follows the rules corresponding to each particular level of sociological integration, so their differentiation not only results from differential perception of the crop categories, but also from the process of their vertical transmission within the group. While the former affects the crop diversity through individual farmers' selection, the latter affects migration, mainly by limiting seed-mediated gene flow among farmer groups. Thus, the perception of group membership *per se* (social identity) becomes central in the analysis of crop genetic diversity.

4.2.1. Basic Levels of Sociological Integration

At the individual farm level, the main parameter limiting seed-mediated gene flow is the seed saving rate. Several studies show that farmers usually produce 75–80% (range between 58% and 99%) of their seeds on their own farm, which of course strongly reduces the proportion of acquired seeds (Table 1). Moreover, these on-farm studies show that seeds are more often acquired from within the community than outside, or from the "informal" as compared to the "formal" (commercial) sector [84,116,117]. Unfortunately, these in-out typologies rarely consider characterizing the social network and thus ignore the possibility that the "informal" sector can be itself formally structured from an anthropological point of view. Indeed, the seed circulation system logically operates according to the prevailing exchange system *within a given social organization* [118], so farmers must be characterized sociologically to understand the structure and functioning of the seed system.

Table 1. Sources of seeds in traditional agriculture.

Country	Crop	Farmer saved seeds	Family and neigbourhood	Total	References
Burkina Faso	Sorghum	70%–99%	NA	70%–99%	[119]
Costa Rica	Maize	79%	19%	98%	[117]
Costa Rica	Beans	58%	21%	79%	[117]
Guatemala	Maize	59%	31%	90%	[22]
Honduras	Maize	75%	13%	88%	[117]
Honduras	Beans	79%	15%	94%	[117]
Mexico	Maize	90%	9%	99%	[120,121]
Mexico	Maize	58%	34%	92%	[75]
Mexico	Maize	79%	NA	79%	[5]
Mexico	Maize	NA	87%	87%	[76]

Table 1. *Cont.*

Country	Crop	Farmer saved seeds	Family and neigbourhood	Total	References
Mexico	Maize	NA	95%	95%	[79]
Mexico	Maize (Tzeltal)	84%	9%	93%	[24]
Mexico	Maize (Tzotzil)	87%	10%	97%	[24]
Mexico	Maize	76%	11% *	87%	[23]
Mexico	Maize	76%	21%	97%	[84]
Nicaragua	Maize	81%	12%	93%	[117]
Nicaragua	Beans	72%	14%	86%	[117]
Peru	Potatoes/ulluco	91%	6%	97%	[19]
Sierra Leone	Rice	70%	NA	70%	[89]

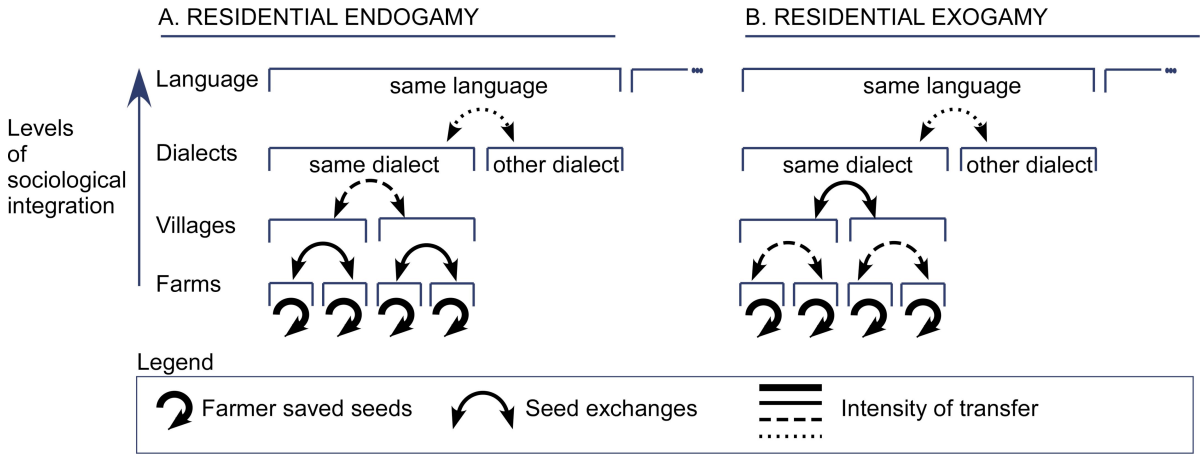
* This percentage refers only to family members that made up 47.5% of seed providers.

Beyond the individual farm level, a few studies have shown the interest of considering the social organization, characterizing the protagonists and the relations they maintain beyond the agricultural domain. The fact that exchanged seeds are mainly obtained through trusted persons, members of the same family, the same village or the same community has been documented for maize in Mesoamerica [121,22]; Andean tubers in Peru [19], sorghum in Ethiopia [122]; and rice in Gambia [116]. Badstue *et al.* [121] characterize more precisely the persons from whom the 10.3% off-farm seeds are obtained in a Mexican community: family members (46.5%), *compadres* (4.7%), neighbors (1.3%), friends (7.2%) and acquaintance (29.6%, a category including sharecropper relations and owners of neighboring fields). Where several ethnic groups live in the same village, the seed exchanges are preferentially (up to 90%) concluded with members of the same ethnic group [117,119]. In the end, seeds are rarely supplied by outsiders. In the cases studied by Badstue [121] only 1% of the seeds come from such sources. Badstue *et al.* [23] describe more precisely why informal seed systems are mostly based on traditional social alliance and family relations. In their case study, farmers clearly distinguish maize seeds for planting and grain for consumption. The quantity of seed involved in farmer-to-farmer transactions is "often quite small". However, when farmers have to replace lost seed, seed quality can be neither guaranteed nor tested (seed is not "transparent"), and "farmers depend largely on the quality of the information offered by the seed provider" [23]. Thus, trusted transactions must be already embedded into a concrete social network, interpersonal relations being experienced inside as well as outside the agricultural domains, which cannot be studied as a separate sector, but as a component of a whole.

Another interesting example of the embeddedness of seed exchanges in the social organization is provided by the observations of Longley [89] in Sierra Leone, showing how "the geographical patterns of marriage also map the pathways along which seed rice varieties travel". The Limba tend to marry individuals from the local area, whereas Susu marriage networks are geographically more extensive. As a result, Susu farmers acquire larger proportions of non self-saved rice seed from outside their own village as compared to the Limba. Even so, friends and family are still favored sources as compared to traders. This example introduces the importance of residential endogamy as a social factor affecting the orientation of the seed exchange system and, by the way, the geographic organization of crop genetic diversity. Figure 2 shows that, in the case of a high residential endogamy rate (marriage

concluded within the same village), seeds obtained from the in-law family originate from the same residential group, favoring genetic differentiation among villages. Conversely, a low residential endogamy rate would induce an out-of-village-oriented seed exchange, and the social network structure would be necessarily "decoupled" [87]. In the latter case, crop genetic differentiation can be expected to be lower among villages than within villages. Thus, the seed system must not be analyzed only in terms of geographic distance, but also through organizational modalities of human collective life, basically, filiation, residence, marriage and inheritance rules.

Figure 2. Expected effects of residential endogamy on the orientation of seed exchanges and spatial distribution of crop genetic diversity. Pattern **(A)**: Baka communities (Cameroon). Residential endogamy (husband and wife are from the same village): seeds are obtained from the in-law family which is from the same village; this favors genetic differentiation among villages; Pattern **(B)**: Nzimo communities (Cameroon). Residential exogamy: (husband and wife are from different villages): seed exchanges are oriented outwards, which results in lower genetic differentiation among villages. Patterns A and B produce different structures of crop metapopulations, affecting crop genetic organization at different levels of sociological integration.

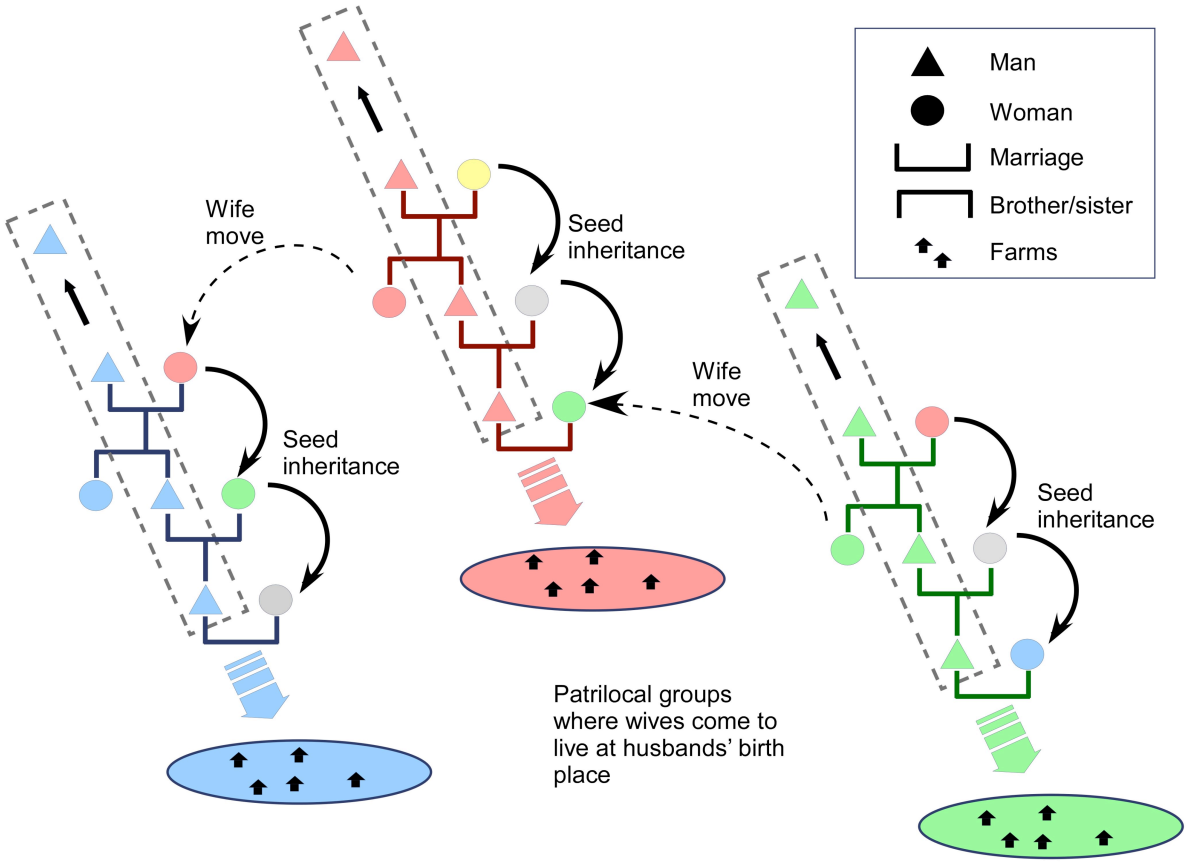


Affiliation rules combined with residential rules and gender role affect the geographic organization of crop genetic diversity. Where crop management is a female domain, matrilocal residence will allow seeds to stay in the village, while patrilocal residence will favor seed diffusion among villages, through women mobility. The latter trend is reinforced when the residential group is constituted by one lineage (localized patrilineage, e.g., Nzimo, Cameroon), implying marriage out of the residential group. Indeed, as patrilineal descent groups are exogamous, marriages have to be concluded with women from other villages. In the other case, if the village is constituted of several lineages or clans, residential endogamy is possible and part of the seed exchanges, through in-law family relations, can be concluded within the village.

The latter analysis shows that seed systems can be both geographically open, which is always true up to some level, and socially closed with marriage and kinship ties or other social relations linking providers and recipients, spatially distant or not. Such variation is necessarily expressed in space [19,20,22].

Figure 3 presents an example of the combined effects of filiation, post-marital residence and seed inheritance on the spatial structure of crop genetic diversity. This example shows their importance for both the definition of crop genetic diversity sampling strategies and the interpretations of studies where social relations have not been characterized prior to sampling.

Figure 3. Vertical transmission of seeds in Muthambi communities on Mount Kenya. Colors represent different clans. Those communities are characterized by patrilineal filiation i.e. men live in the clan they were born and wives leave their own clan to join that of their husband when they get married. Wives establish their first fields with sorghum seeds traditionally obtained from their mother-in-law. It follows that the founding germplasm remains in the same residential group over generations, thus contributing genetic adaptation to the local environment.



4.2.2. Higher Levels of Sociological Integration

The vertical transmission of crop genetic diversity is even more prevalent at higher sociological levels, as the seed system is necessarily more within-oriented with increasing sociological integration level, as shown in Figure 2. Thus, crop genetic diversity and its organization may be interpreted in the light of cultural transmission theories for cultural traits, by considering farmer varieties as cultural objects. The crop genetic sampling strategy must then be based on the cultural identity of farmers, beyond the circle of personal relationships.

The importance of the higher levels of farmer social differentiation (beyond families and residential groups) was first realized empirically by plant breeders, when it appeared to be a limiting factor for

improved seed diffusion. Indeed, social differences among communities and ethnic boundaries can slow down the diffusion process and reduce the general impact of breeding programs [117,123]. Among these social differences, linguistic differentiation is essential. There is no seed exchange without information exchange and communication is possible only if provider and recipient speak the same language. Inter-groups exchange could be common between allied villages speaking the same language, and rare or inexistent between two differentiated linguistic groups. Of course, vehicular language can be used to link two distinct vernacular linguistic groups, but the fact that vernacular languages have differentiated the two groups remains an important marker of farmers' social organization resulting from historical processes and, thereby, an important factor structuring exchanges and crop genetic diversity. As noted by Harlan and Stemler [38], "correspondence between the distribution of the basic races of sorghum and the distribution of the major linguistic groups of indigenous Africans may be not fortuitous. Guinea is a sorghum of the Niger-Congo family, kafir a Bantu sorghum. Durra follows the Afro-Asian family fairly closely, and caudatum seems to be associated with the Chari-Nile family of languages". According to the same authors, more detailed study of minor variations in sorghum may prove this correspondence revealing with respect to human history and ethnic isolation.

The relation between linguistic community and germplasm exchange is bidirectional. Studying rice cultivar names in Gambia, Nuijten and Almekinders [116] observed that their uniformity reflects the intensity of seed exchange. "When there is limited inter-village seed exchange, a variety is likely to end up with different names in different villages. In the case of multiple seed exchanges of the same variety between two villages, (…) that variety may obtain the same name in both villages". Thus, farmer variety names are exchanged as other language elements. Again, we observe how crop germplasm is treated in the same way as other cultural objects.

Very interestingly, this principle can be applied at different scales and levels of sociological integration. We come here to the basic principle of the method of historical linguistics: the similitude of words used reflects the intensity of past contacts and the importance of the common historical heritage, which allows to develop a strong parallel between the vertical transmission of words (inheritance within speech communities) and the vertical transmission of crop germplasm, both phenomena concurring to the organization of human societies and their crop genetic resources. Applying phylogenetic methods to Bantu languages, Holden [96] confirmed the prevalence of social factors over geographical barriers in maintaining distinct speech communities and observed how language evolution was consistently correlated to the archaeological evidence for the spread of farming across Bantu-speaking Africa. Similarly, Philippson and Bahuchet [124] could use the linguistic method for tracing the diffusion of crops originating from America through their transmission in the Bantu languages of Africa. In Polynesia, bread fruit diffusion, as reconstituted with genetic markers, also reflects the human peopling of the archipelago [125]. Perrier *et al.* [126] propose a reconstruction of the movement and cultivation of bananas from New Guinea to West Africa during the Holocene, based on a combination of genetic, linguistic and archaeological data.

The social structuring of diversity is also particularly noticeable in animal populations due to greater mastery of their reproduction. The interdependence relationship established between cattle and man has made it possible to trace back the migratory channels taken by the pastoral societies that introduced them into Africa from the genetic imprint remaining in existing cattle populations [127].

That inference is possible because the diversity of that resource is socially structured. Despite the time that has passed since their introduction, cattle cross-breeding has never blurred the original trace left on a molecular level, precisely because herd management is clearly differentiated among human groups. In this and other cases [128,129], the history of domesticated resources and the history of the human groups ensuring its perpetuation from generation to generation shed light on each other because domesticated resources have been affected by the conservatism of vertical transmission.

5. Conclusion

While vertical transmission, together with many cultural traits, including agricultural practices, plant uses, and knowledge, affects crop genetic diversity, the resulting structure is necessarily expressed in space and time. Indeed, human groups also utilize spatial distribution to signalize their differentiation. Then, environmental adaptation will also play a more prominent role at higher levels, as two groups living in different, distant, environments should exploit different resources. This interaction poses a methodological problem for the study of crop genetic diversity at levels where the impacts of social and environmental factors cannot be distinguished. Indeed, an ideal situation would allow a double comparative approach, by a comparison of different groups in the same environments and comparing the effects of different environments exploited by a same group. This is generally feasible at small to medium scales, as, for example, in the situation described by Zimmerer [19] in the Peruvian Andes. We are also studying sorghum diversity among and within related ethnolinguistic groups distributed along an altitudinal gradient on Mount Kenya. The simultaneous control of social and environmental factor is more difficult at larger spatial scales, because of the correlation between distance and environmental variation. However, the G × E × S interaction model can be tested in wide regions with similar ecological conditions, as in Sahel, where ethnolinguistic groups are distributed across precipitation gradients that constitute most of environmental variation (see sorghum studies of Ollitrault *et al.* [29] and Deu *et al.* [62]).

The link between linguistic, cultural, and biological diversity has been described at the interspecific level [130]. In the present paper, we have revised, among the main aspects structuring human societies, those that are most likely to affect the organization of crop genetic diversity, in both social and geographical spaces. First, rules of filiation, inheritance and marriage mostly play vertically in the transmission of seeds. These rules combine with those of residence in determining the spatial distribution of both people and their crop genetic resources, residential endogamy favoring a centripetal orientation of exchange systems. In this respect, seeds and crops must be analyzed as social objects.

All studies of farmers' seed sources show the importance of self-produced seeds and within-community exchanges, which constitutes another strong element of verticality. Several authors have interpreted their results assuming significant seed exchanges among communities. Still, this hypothesis has not been convincingly supported and is subject to debate. A major point in this debate is that seeds are but one component of social networks of exchange. Given their importance for the farmers' success and subsistence, communication and trust are even more important and the main restriction to wide seed exchanges is the risk accompanying foreign seeds.

After seed inheritance and seed saving, a third important element of verticality lies in the necessary consensus on the linguistic sign, *i.e.*, the unambiguous link between a signifier and a signified [131],

within farming communities, which is a prerequisite to the intergenerational transmission of knowledge, including all elements of folk taxonomy. Perception of crop diversity and their conservation through phenotypic selection cannot be conceived out of this cultural framework.

Our review of two widely studied traditional crop models has shown us that sampling strategies have often overlooked the role of society. However, when ethnic factors have been partially taken into account, as in the study of Deu *et al.* [62] or those of Brush and Perales [25] and Benz *et al*. [79], diversity studies have brought significant progress in our understanding of social and biological processes and their interactions. But the sampling strategy is usually validated *a posteriori*. As stated by Sagnard *et al.* [132], the observed crop diversity results from a historical and dynamic evolution, where "the number of processes involved and their interaction allow the same image to be produced from different combinations of factors". The analysis of a given genetic organization is thus confronted to the limits of final cause reasoning, where the geneticist measures the impact of the factors he/she has selected, without having the possibility of observing their action directly and without excluding that other factors can be at work. Interestingly, this situation is also true for anthropologists studying cultural diversity. Indeed, human group diversity also results from historical processes implying many factors and their interactions, and a hypothetic-deductive approach through comparisons is also needed.

At the functional level, the factors explaining the crop genetic differentiation in biology and those explaining social differentiation of farmers in anthropology are analogous with vertical and horizontal transmission processes. Indeed, gene inheritance is a vertical process, maintaining differentiation between populations, while gene flow is a horizontal one that, in the absence of barriers, leads on the contrary to crop genetic homogenization. On the social side, cultural differentiation processes are similar, because of the existence of vertical and horizontal transmission processes, as defined by Cavalli-Sforza and Feldman [94]. Thus, farmers' cultural and crop genetic differentiation could be analyzed with the same conceptual frame using the genetic sampling strategy as the focal point of interdisciplinarity.

For an efficient integration of the relevant social factors, we have proposed modifying the classical "G × E" approach by a "G × E × S" one, where the social component is explicitly taken into account. As stated above, this imposes a sampling strategy respecting the linkages between given social groups and their crop populations, so as to test the social identity of farmers as an organizing factor of crop genetic diversity. In other words, we recommend a joined farmer/crop sampling strategy, the farmer with its social characteristics becoming the factor, and the crop population characteristics, the dependent variables. In this strategy, environmental variation should be as independent of social group distribution as possible, so avoiding confusion in the interpretation of results. Such a design imposes a thorough analysis of the social groups involved, aiming at understanding social structures and historical factors at play at all scales. According to the means and specific objectives of the study, the most significant level of sociological integration/differentiation must be identified.

In these conditions, it should be possible to show that cultural diversity works hand in hand with agrobiological diversity. This hypothesis is confirmed *a contrario* in the recent history of western agriculture. For example, while French farmers massively adopted homogenous cultivars acquired from breeding companies (hybrid maize, triploid beet, wheat pure lines, *etc*.), they became socially more homogenous as actors of a widespread intensive agricultural system [18].

The understanding of the social drivers of crop genetic diversity, as explicited in the G × E × S model, is essential in participatory plant breeding, ensuring the efficient selection of consensual phenotypes, and promoting their diffusion through an adequate choice of participants. Here again, the parallel with the network model may be fruitful in the development of strategies allowing to exploit both strong links within solidarity groups, and weak links among them.

While biologists must take into account the social organization of human societies in the analysis of crop genetic differentiation, the anthropologists may benefit from the reverse proposal. We have mentioned the Hannote *et al.* [127] study where the genetic imprint of ancient cattle migrations allows inferring the migratory channels of African pastoral societies thanks to the anthropological fact that societies have maintained their differentiation up to the present. As hypothesized for sorghum in Africa [33,37-39,62], and bread fruit in Polynesia [125], similar approaches may be envisaged with other plants, using crop molecular markers as historical correlates of past human relations.

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Article

Distribution of the Genus *Passiflora* L. Diversity in Colombia and Its Potential as an Indicator for Biodiversity Management in the Coffee Growing Zone

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Abstract: Analysis was made of 3,923 records of 162 wild *Passiflora* specimens to assess the distribution of their diversity in Colombia, identify collection gaps, and explore their potential as indicator species. Despite variable collecting density among and within biogeographic regions, the Andean region clearly presents a higher species richness, particularly in the central coffee growing zone and the departments of Antioquia, Cundinamarca and Valle del Cauca. The elevational distribution of diversity shows a small peak below 500 m, and two higher ones between 1,000–2,000 and 2,500–3,000 m. This pattern corresponds to divergent adaptive trends among infrageneric divisions. The analysis on 19 climatic variables showed that the two principal variance components, explaining 77 percent of the total, are respectively associated with temperature and precipitation, without influence of seasonality. Distribution parameters allow recognizing more than 36 narrow endemics. Prediction of species distribution showed nine areas with very high richness (predicted sympatry of 41 to 54 species) in the Andean region, three of which correspond to collection gaps. Endemics were not particularly frequent there, so a

prioritization of protected areas based on species richness would not favor their conservation. The sites with high *Passiflora* diversity are poorly represented in the current system of protected areas. Instead, their striking correspondence with ecotopes of the coffee growing zone imposes a conservation strategy integrating agricultural and environmental management at the landscape level. Reciprocally, several traits of *Passiflora* species make them particularly suited as indicators for any effort of conservation or restoration in this region of importance for the country.

Keywords: Andes; coffee growing zone; Colombia; biodiversity indicators; endemism; geographic information systems

1. Introduction

Colombia is divided into five main biogeographic regions [1]. The Andean region presents a highly diverse topography (100–5,400 m), with three mountain ranges, the Eastern, Central and Western Cordilleras, separating two main inter-Andean valleys from the other regions. The uplift of the Andes created new habitats and increased local isolation, favoring high speciation rates in many taxa [2]. The continuously humid climate of the Amazonian and Orinoquian lowlands and the extremely wet climate of the Pacific region contrasts with the drier and more seasonal climate of the Caribbean. As a result, the Colombian flora includes some of the world's most diverse groups of vascular plants, with 51,220 documented species [3-5]. It is hoped that most of this floristic richness is located in the protected areas that cover 365,120 km^2, approximately 32 percent of the territory [6], falling under different categories of protection, including Natural National Parks, Flora and Fauna Sanctuaries, Natural National Reserves, Unique Natural Areas, Park Ways and Indigenous Areas, among others. Smaller forest reserves have also been created to protect river basins for water supply. On the other hand, destruction of many natural habitats has drastically affected species, often reducing their historical ranges to a set of small, fragmented populations. Such alteration is predicted to lead to substantial extinction in the near future [6]. Within the field of conservation biology as a whole, and protected area management in particular, it is becoming increasingly urgent to develop spatial and temporal predictions of how significant environment changes, and, particularly, multiple anthropogenic threats, may affect the abundance and distribution of species [7,8]. Bioclimatic modeling can provide first-cut estimates of risk of biodiversity loss even where species distribution data are relatively poor [8].

Many conservation biologists have focused their attention on areas presenting high levels of endemism and diversity, and experiencing a high rate of loss of ecosystems. Such regions concentrating biodiversity under threat are defined as biodiversity hotspots, representing priorities for conservation actions [9]. The tropical Andes are considered one of these hotspots, as they support almost half of the Neotropical biodiversity [10]. However, the application of this concept in the case of Colombia implies the development of wide studies to investigate the distribution of biodiversity, at an operational resolution level across the country. Complete inventories are not realistic at that scale, so other approaches have been taken to exploit incomplete biodiversity data, combining remote sensing and field sampling/inventories of indicator taxa at different scales [11]. We proposed the use of

climatic niche modeling and tested the potential of *Passiflora* as an indicator of biodiversity in Colombia, as Passifloraceae represent several interesting traits in terms of diversity, adaptation and evolution.

Indeed, Colombia is particularly rich in Passifloraceae, with 167 species from *Ancistrothyrsus* (2), *Dilkea* (4) and *Passiflora* (162) genera, mostly in the Andean region (123 species). The country has 57 endemic species, 95 percent of them Andean, implying a high extinction risk as this region is the most densely populated and disturbed, particularly the coffee growing zone [12]. According to the Von Humboldt Institute, the Universidad Nacional de Colombia [13], and Ocampo *et al*. [12], more than 100 Colombian Passifloraceae species are threatened to some degree, and three species are considered extinct.

Neotropical Passifloraceae include about 650 species from the genera *Ancistrothyrsus*, *Dilkea*, *Mitostemma* and *Passiflora* [14]. The largest one is *Passiflora*, with *ca.* 575 species distributed in a wide range of habitats, from humid rain forests to semi-arid subtropics. Most of them are herbaceous or woody vines, while a few are trees or shrubs. More than 80 species produce an edible fruit, the most interesting ones belonging to subgenera *Passiflora* and *Tacsonia* [15,16]. Among them, are the yellow and purple maracuja, *P. edulis* Sims, with a world production estimated at more than 805,000 tons [17], and more than 13 species/forms present on the national or local markets of Colombia [12]. *Passiflora* species also present ornamental and pharmaceutical interest [16]. Killip's [18] classification divided *Passiflora* into 22 subgenera. It was amended by Escobar [19,20], who merged two subgenera and proposed a new one, and by MacDougal [21], who revised subgenus *Plectostemma*, restoring its ancient name *Decaloba*. In 2003, Feuillet and MacDougal [22] proposed a deeper revision, recognizing only four subgenera, *Astrophea*, *Decaloba*, *Deidamioides* and *Passiflora*. This proposal has been partially justified by molecular data [23-26], however further studies are still needed for understanding Passifloraceae diversity and evolution.

As vines, most *Passiflora* species have adapted to many different habitats, particularly for their support. They are medium-lived organisms depending on longer-lived trees and shrubs, which makes them responsive to both medium and long-term changes. They also show high levels of co-evolution with their herbivores, particularly *Heliconius* butterflies [27], and some species even exhibit elements of the carnivory syndrome [28]. They have developed mutualism with protector insects as nectar-feeding ants [29], and with a wide range of pollinators, including small and large insects, birds and bats [30,31]. Finally, given its economic importance, the genus *Passiflora* constitutes an important genetic resource, and the characterization of wild and cultivated populations is seen as a priority for Andean countries because of its potential for development and crop diversification [32]. Strategies for conservation and improvement are needed to optimize the use and conservation of this resource.

Biodiversity data have been traditionally produced through a variety of complementary approaches using field survey and sampling, museum records, botanical collections, and, in recent times, spatial analysis of data integrated within Geographical Information Systems (GIS). In each area, the combination of geological, edaphic, climatic, ecological, historical and anthropic factors produces a unique range of constraints defining patterns of diversity [33]. GIS allow building maps of species richness, potential distribution and endemism, prioritizing areas for conservation based on principles such as complementarity, and assessing the completeness of existing protected areas networks [34].

Several methods use climatic variables as the principal drivers of herbarium or collecting data, generating information for diversity studies and conservation actions [35,36]. Such modeling tools have been applied to problems of phytogeography [37,38], conservation [39,40], evolutionary ecology [41], invasive or endemic species management [42-44], potential areas for plant collection [45,46] and the effect of climate change on crop wild relatives [47]. In *Passiflora*, Segura *et al*. [48] mapped the potential distribution of five species of the subgenus *Tacsonia* and produced evidence of intra-specific variation in climatic adaptation along the Andes, from Colombia to Peru.

The present study was conducted through (1) assessing the geographic distribution of Colombian Passifloraceae; (2) analyzing it in terms of species richness across the territory; (3) inferring the potential distribution of each species with predictive distribution models; (4) summing these spatial predictions to produce a map of potential diversity; and (5) locating collecting gaps by detecting those areas where *Passiflora* species are likely to occur but have not yet been collected. Combining these results permits an analysis of the current status of *in situ* and *ex situ* conservation of *Passiflora* in Colombia. It also provides elements to evaluate the potential of this group as an indicator for the detection of biodiversity hotspots and monitoring of conservation/restoration efforts.

2. Material and Methods

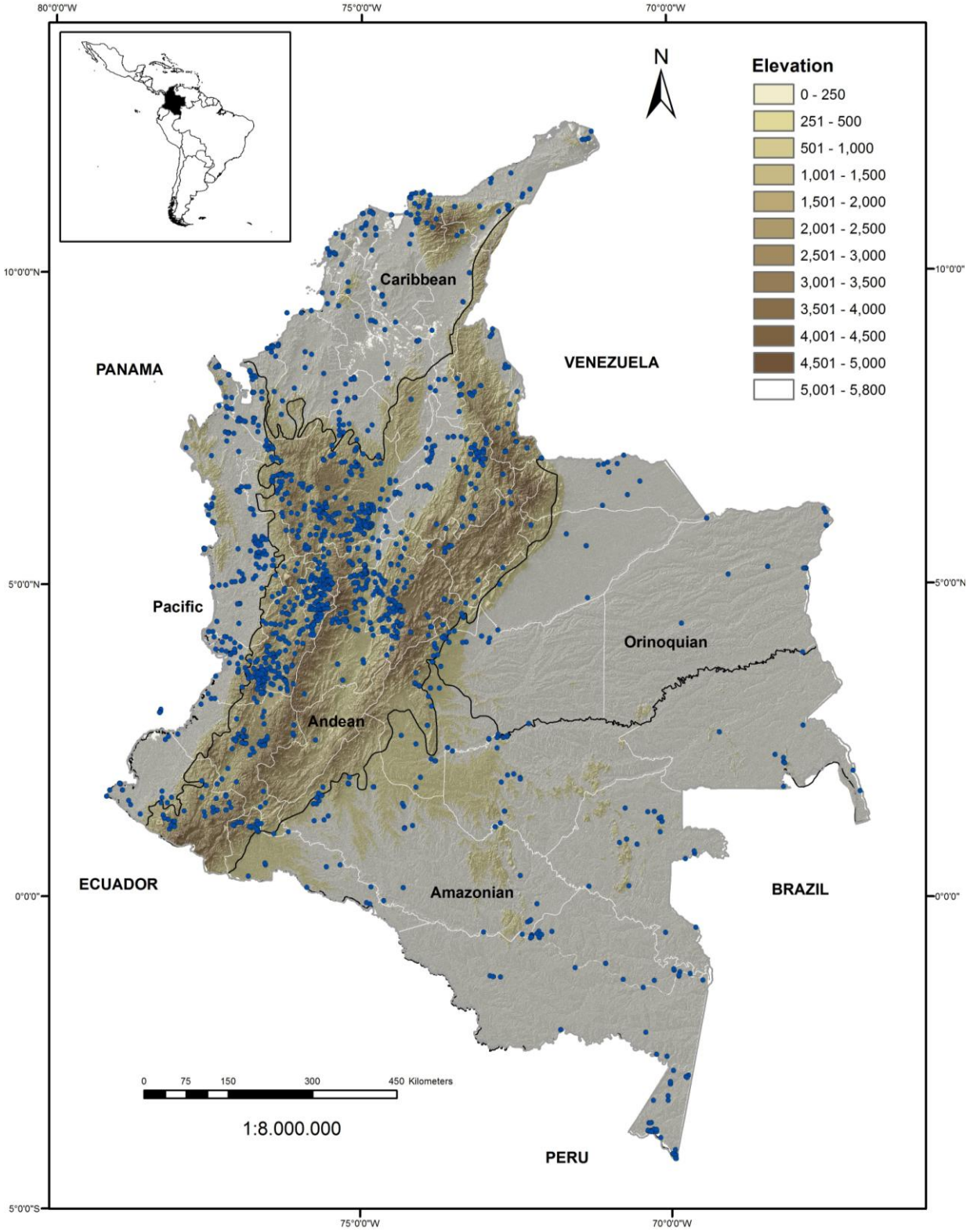
2.1. Geography and Climate

Colombia is located in the north of South America, between 12°26'46" N and 4°13'30" S and between 66°50'54" W and 79°02'33" W, covering an area of 1,141,748 km^2, with altitudes ranging from the sea level to 5,775 m [1]. It is divided in 32 departments (see Supplementary Figure 1: Colombia's geopolitical division in 32 departments and biogeographic division in five regions.). Figure 1 shows their distribution among the five biogeographic regions of the country [1]. Colombian climates are tropical, with relatively uniform temperatures throughout the year. Precipitations vary greatly, with some of the wettest parts of the world in the Pacific lowlands (average annual rainfall reaching 10,000 mm) contrasting with extremely dry areas in the coast (<500 mm per year), and show a tendency to increase with altitude.

2.2. Species Distribution and Richness

The original plant dataset consists of the information gathered and georeferenced by Ocampo *et al*. [12] from 3,930 individuals of 167 Passifloraceae species, consisting of 3,330 herbarium specimens (AFP, CAUP, CDMB, CHOCO, COL, COAH, CUVC, FAUC, FMB, HUA, HUQ, JAUM, K, MA, MEDEL, MO, NY, P, PSO, SURCO, TOLI, VALLE and UIS), 555 field records, and 45 records from Killip [18,49], Uribe [50] and Escobar [19,20,51]. The few specimens from genera *Ancistrothyrsus* (three) and *Dilkea* (four) brought too limited information, as compared to *Passiflora*, so they were not taken into account in the analysis presented here.

Figure 1. Collection localities (blue dots) of *Passiflora* specimens used in this study among 32 Colombian departments and five biogeographic regions (see Supplementary Figure 1).



Species distribution was plotted on dot-maps using the DIVA-GIS software and quantified by their maximum distance (MaxD) and circular area (CA*r*) according to Hijmans *et al.* [52]. For each species,

MaxD is the longest distance between any pair of observations, and CA_{50} was calculated by assigning a circle of radius 50 km to each observation and calculating the area covered by all circles. As in a previous paper [12], we used the following threat criteria: a number of observations under six characterizes rare species, MaxD under 100 km and CA_{50} under 20,000 km^2 characterize narrow endemics.

Species richness was calculated as the number of species within a defined area, superimposing species location maps, using the point-to-grid richness analysis tool in DIVA-GIS with a $0.1 \times 0.1°$ grid (*i.e.*, 12 × 12 km at the Equator). The circular neighborhood option was applied with a 2 ° radius [37] to eliminate border effects due to assignation of the grid origin.

2.3. Climatic Adaptation and Modeling

Climatic models were developed to predict species occurrence, with DIVA-GIS. This package uses WorldClim data [52], consisting of global climate surfaces with a 30" grid resolution (*i.e.*, 1×1 km at the Equator), derived from a network of over 12,500 meteorological stations across Latin America, 1,479 of them in Colombia. For each collection site, 19 bioclimatic variables (derived from 12 monthly means for temperature, rainfall and diurnal temperature range according to Busby [53]) were extracted. Principal components analysis (PCA) was performed on the resulting dataset, applying a varimax normalized rotation. For readability, the centroid, *i.e.*, the arithmetic average of the factor scores, was used to represent each species climatic preferences.

Potential species distributions were mapped by extrapolation, using the 19 bioclimatic variables and the DIVA-GIS BioClim method for the 80 species with more than 10 observations. BioClim was chosen because it is a robust methodology, requiring presence-only data [54]. Unfortunately, many of the omitted 85 native species, too poorly represented for reliable results, are endemic and/or rare species. Finally, an analysis of complementarity [55] was applied to identify the lowest number of protected areas needed for the conservation of native *Passiflora* species.

3. Results and Discussion

3.1. Distribution of Observations and Species Richness/Diversity

Figure 2 and Table 1 show the distribution of collection/observation points. The Andean region of Central Colombia is by far the most densely explored, particularly the central coffee growing zone (Quindío, Caldas and Risaralda; 18.93 to 77.20 observations/1,000 km^2) and the three large departments of Antioquia, Valle del Cauca and Cundinamarca (12.45 to 19.82 observations/1,000 km^2). By comparison, the northeastern Andes (Boyacá, Santander, and Norte de Santander) and the central department of Tolima appear less well explored (3.59 to 9.39 observations/1000 km^2). The situation is more difficult to appreciate in the southern Andes, as the southern departments of Cauca and Nariño also belong in good part to the Pacific region. However, they show a collection density only slightly superior to that of Chocó, which indicates that they have also been less explored than the central Andes. The situation is heterogeneous in the Caribbean, with only two of its seven departments exhibiting more than three observations/1,000 km^2 (excluding the atypical case of the small San Andrés and

Providencia islands). Finally, the Amazonian and the Orinoquian are by far the least explored biogeographic regions of the country, although they cover half of its area.

The mean number of observations per species also reflects variation in exploration among departments (Table 1), confirming the much denser exploration in the Andes of Antioquia, Cundinamarca and Valle del Cauca (more than seven observations/species) and in the Pacific region, while this ratio takes much lower values in the other regions. However, the relation between exploration density and this indicator is not simple, as the numerous observations in the central coffee growing zone are distributed among a very wide diversity of species, so the mean number of observations/species is not as high as could be expected for such densely explored areas.

Figure 2. Species richness observed for *Passiflora* in 0.1 × 0.1 ° grid cells in Colombia (162 species). Points on the map represent sites of collection.

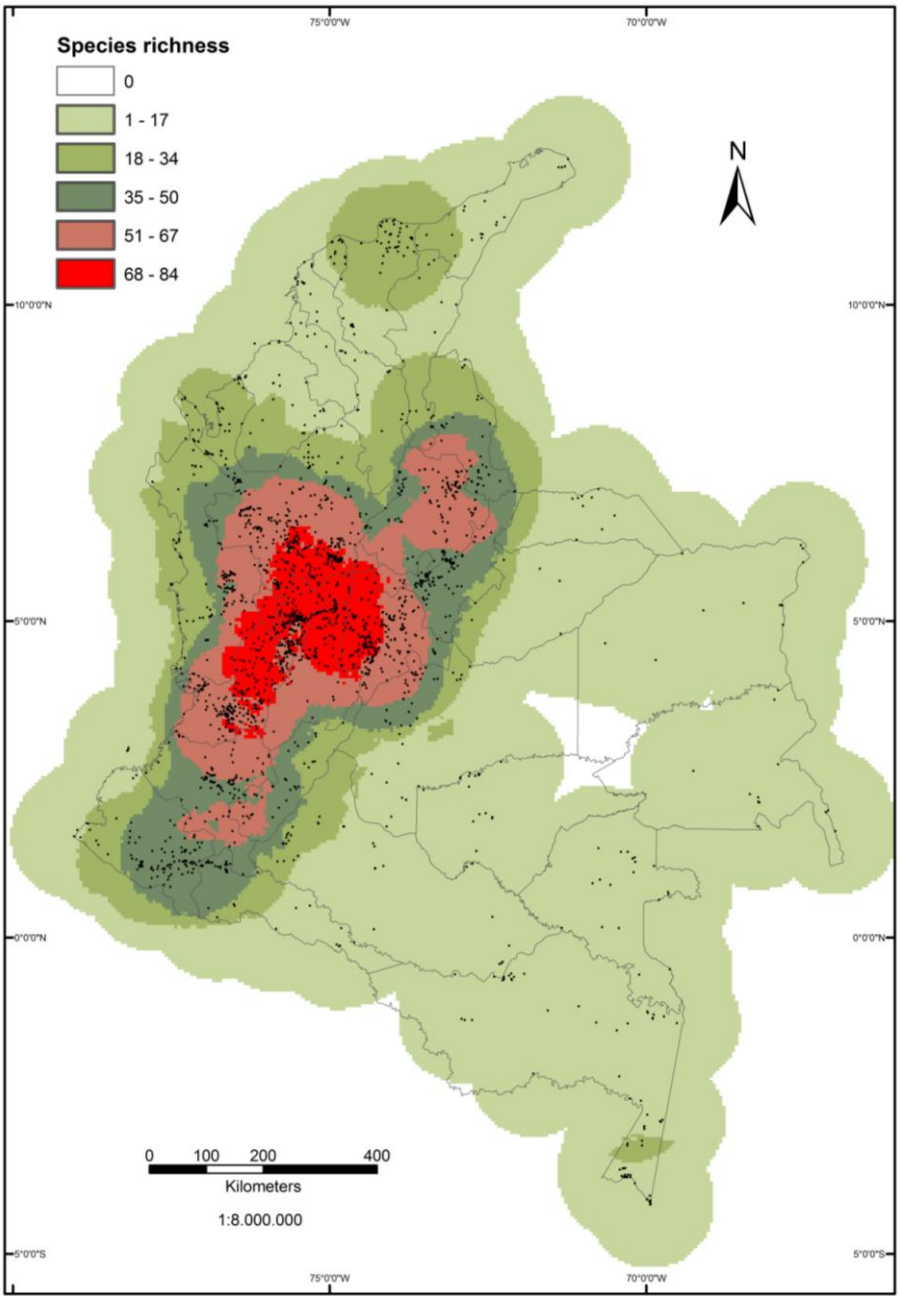


Table 1. Number of observations, species, rare and endemic *Passiflora* species by Colombian division (see Supplementary Figure 1).

Biogeographic region/ department	Area (km^2)	Nb. observ.	Nb. observ./ 1,000 km^2	Total Species	Total species/ 1,000 km^2	Total species/ Log. area	Observ./ species	Rare species	Endemic species
Andean									
Antioquia	62.869	783	12.45	68	1.08	14.171	11.51	28	6
Boyacá	23.012	145	6.30	36	1.56	7.502	4.03	14	1
Caldas	7.291	245	33.60	36	4.94	7.502	6.81	14	1
Cundinamarca	23.942	419	17.50	53	2.21	11.045	7.91	23	0
Huila	18.331	62	3.38	22	1.20	4.585	2.82	18	0
Quindío	1.943	150	77.20	38	19.56	7.919	3.95	25	0
Norte de Santander	22.007	79	3.59	36	1.64	7.502	2.19	25	0
Risaralda	3.592	68	18.93	24	6.68	5.002	2.83	20	0
Santander	30.537	207	6.78	48	1.57	10.003	4.31	31	3
Tolima	22.672	213	9.39	43	1.90	8.961	4.95	27	4
Andean and Pacific									
Cauca	30.985	161	5.20	42	1.36	8.753	3.83	24	1
Nariño	32.046	170	5.30	44	1.40	9.170	3.79	27	0
Valle del Cauca	21.195	420	19.82	56	2.69	11.670	7.38	28	1
Pacific									
Chocó	46.530	210	4.51	39	0.84	8.356	5.38	23	1
Caribbean									
Atlántico	3.319	18	5.42	7	2.11	1.459	2.57	5	0
Bolívar	26.469	33	1.25	15	0.57	3.126	2.20	9	1
Cesar	22.213	13	0.59	10	0.45	2.084	1.30	9	0
Córdoba	25.020	33	1.32	9	0.36	1.876	3.67	6	0
La Guajira	20.848	21	1.01	12	0.58	2.501	1.75	9	0
Magdalena	22.742	84	3.69	31	1.36	6.460	2.71	19	1
S. Andrés y Providencia	53	4	75.47	2	37.74	0.417	2.00	2	0
Sucre	10.917	6	0.55	3	0.27	0.625	2.00	2	0
Orinoquian									
Arauca	23.393	10	0.43	6	0.26	1.250	1.67	3	0
Casanare	44.428	4	0.09	4	0.09	0.834	1.00	4	0
Meta	85.286	85	1.00	24	0.28	4.930	3.56	14	0
Vichada	100.242	16	0.16	9	0.09	1.876	1.78	6	0
Amazonian									
Amazonas	109.665	85	0.75	16	0.15	3.175	5.31	14	0
Caquetá	91.725	46	0.50	17	0.20	3.425	2.71	13	0
Guainía	70.691	16	0.23	10	0.14	2.084	1.60	9	0
Guaviare	55.391	27	0.49	14	0.25	5.418	1.93	11	0
Putumayo	24.885	56	2.25	26	1.04	2.918	2.15	20	0
Vaupés	54.135	34	0.63	19	0.36	4.014	1.79	10	0

This variation in exploration of the Colombian territory is partly due to difficulty of access and/or social conflict. Data are poor and misleading in lowland forests, collections being limited along rivers in the Orinoquian and Amazonian and rare roads in the Pacific. Social conflict is the prevalent cause in the less explored Andean departments (Tolima, Santander, Norte de Santander and part of Boyacá) and in the Caribbean. Conversely, populated areas, particularly around main cities and their universities (Bogotá, Medellin, Cali, central coffee growing zone), have been densely explored.

However, despite this sampling bias among departments, all observation parameters point to a concentration of *Passiflora* collecting in the central Andes and, within these departments, in the coffee growing zone, a situation explained by both easier access and higher species richness.

Indeed, departments of the Andean region present clearly higher species richness (Table 1). The only non-Andean department showing a comparable richness is Chocó. In the Andes, Antioquia has by far the highest number of species (68), followed by Valle del Cauca and Cundinamarca. Concerning rare species, Santander (northeast) occupies the first place, with 31 species, followed by Valle del Cauca and Antioquia (28), and Nariño and Tolima (27). Thus, there is little doubt that a more thorough exploration north of the Eastern Cordillera (Santander) and south of the Central Cordillera (Tolima) would discover more specimens per species and/or more species. This is even more obvious for the Amazonian, Orinoquian and Pacific departments, given their poor richness/surface and observation/species ratios.

When species richness is related to department size, the most diverse area corresponds to the central coffee growing zone, as this ratio appears to be several times higher in Caldas, Risaralda and Quindío than in the other Andean departments. A precise comparison with departments of other regions is only possible if the species are equally sampled, *i.e.*, if the number of observations per species is equivalent. This is the case for Chocó, Amazonas, and Córdoba, all of them showing a much lower diversity. The map of observed *Passiflora* diversity, as produced by the GIS analysis (Figure 2), confirms the importance of the Andes and the special contribution of the central coffee growing zone.

3.2. Altitudinal Distribution

Ancistrothyrsus and *Dilkea* reach altitudes of 800 m, mostly in the Amazon [12]. In contrast, *Passiflora* is distributed between sea level and 3,700 m. Figure 3 shows a trimodal relationship between elevation and species diversity for this genus, with maximal values below 500 m and in the ranges 1,000–1,500 and 2,500–3,000 m. The species number decreases sharply after 3,500 m until the limit of 4,000 m. To understand better this particular repartition, we have taken into account the complexity of *Passiflora*, gathering its Colombian species into five groups defined on morphological and molecular grounds, and resumed the analysis on these species subsets. This grouping is similar to the four subgenera proposed by Feuillet and MacDougal [22], except that Killip's subgenera *Rathea* and *Tacsonia* are maintained as a distinct fifth group, because of their elongated, red or pink flowers and reduced crown, specifically adapted to pollination by the sword-hummingbird. The four others correspond to (1) subgenus *Astrophea* (trees and shrubs), (2) subgenus *Decaloba sensu* Feuillet and McDougal (Killip's subgenera *Apodogyne, Decaloba, Murucuja, Porphyropathanthus*, *Pseudomurucuja* and *Psilanthus*; mostly species with laminar nectaries, small apetalous flowers, small fruits, and pollinated by bees and small insects, (3) subgenus *Deidamioides sensu* Feuillet and

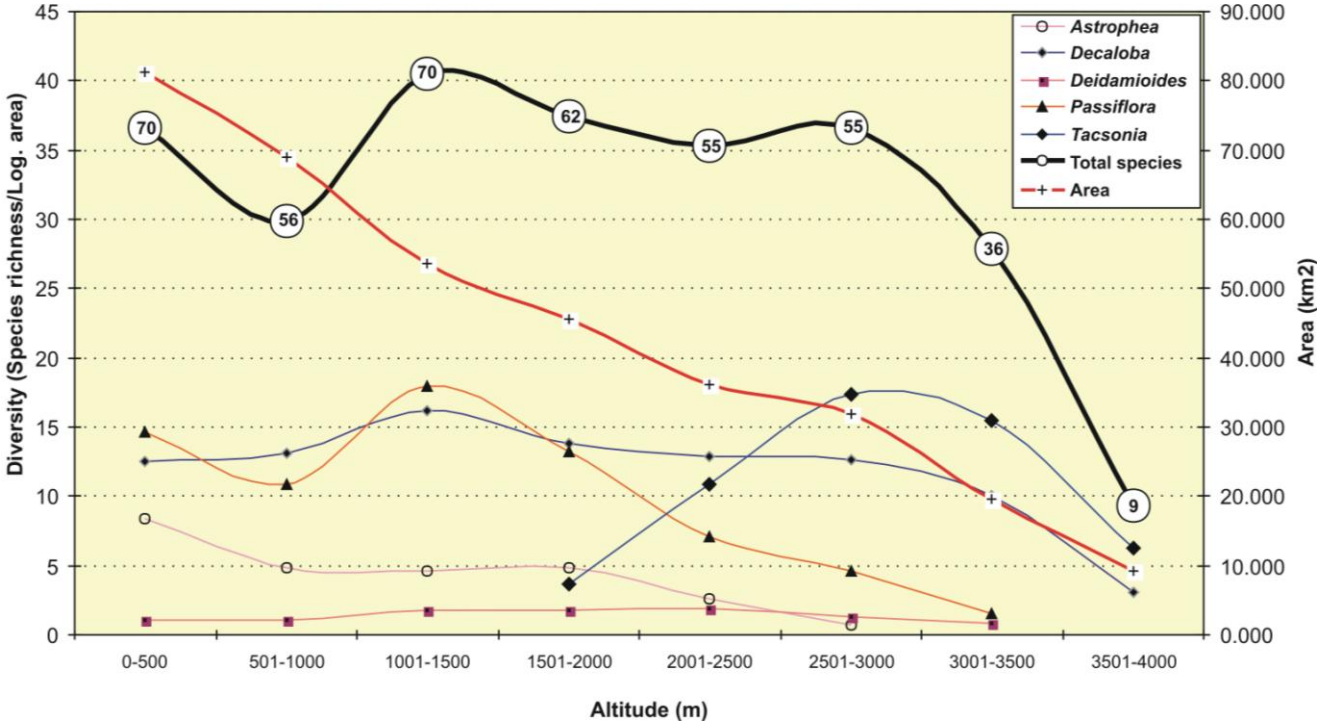
MacDougal (Killip's subgenera *Deidamioides* and *Tryphostemmatoides*), and (4) a *Passiflora*-like group gathering Killip's subgenera *Calopathanthus*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Passiflora*, and *Manicata*, *i.e.*, species with large flowers and fruits, pollinated by large bees or hummingbirds. The comparison between partial curves shows three distinct patterns in the adaptive potential of these groups. *Astrophea* and the *Passiflora*-like group present a bimodal distribution with a first cohort of species adapted to lowlands, below 500 m, with 16 and 28 species respectively, a second one adapted to medium elevations (1,000–2,000 m), and very few species at higher altitudes, with only one record of *P. lindeniana* near 2,700 m for subgenus *Astrophea*, and seven species for the *Passiflora*-like group. The opposite is true for the *Tacsonia* group, showing exclusive adaptation to cool highland climates, as it is typically concentrated above 2,500 m, with a peak at 2,500–3,000 m. Its fast radiation is clearly the cause of the third peak of the global curve. Another pattern is that of the *Decaloba* group, whose range of adaptation extends from 0 to more than 3,000 m, with no lowland peak and a slight peak around 1,000–1,500 m. The few species of the *Deidamioides* group also show a quite uniform distribution from 0 to 3,150 m, mostly in the Pacific and Andean regions. An interrogation remains concerning the first inflexion of the global curve and those of *Astrophea* and *Passiflora*-like groups in the range of 500-1,000 m. Interestingly, Jørgensen [56] reports a bimodal altitudinal distribution of vines in the Ecuadorian flora, with maximal diversity below 500 m and in the 2,000–3,000 m range, and a maximal diversity for *Passiflora* at 2,500–3,000 m. Taking latitudinal variation into account (*Tacsonia* species usually show a higher distribution in Ecuador, with a difference of 300–500 m), this corresponds very well with our observations in Colombia. Considering all Passifloraceae, the variation in number of Ecuadorian species with altitude [57] follows the same pattern as in Colombia. The Ecuadorian richness and high endemism level for *Tacsonia* is another strong point of convergence with the Colombian situation. According to Jørgensen [56], bimodality in altitudinal vine diversity distribution might be due to differential collecting intensity. However, there is no reason to expect a more continuous pattern. Indeed, Kessler [57] showed that there is no common elevational pattern for diversity, but a wide variety of independent patterns at all taxonomic levels, and that endemism appeared highest in the narrowest and most fragmented elevational belts: "The degree to which these influences become visible along the elevational gradient are determined by which combination of species is analyzed". The same conclusion may be drawn within *Passiflora*, taking into account infrageneric divisions. This result restricts the potential use of *Passiflora* species as an indicator group to the Andean region, where they have developed most of their diversity.

3.3. Climatic Requirements

The PCA on the 19 climatic variables evidenced a first factor accounting for half of the variation (49%), strongly correlated with temperature variables (maximum, mean and minimal, but not seasonality in temperature), and a second one explaining 28 percent of the variation, related with precipitation in the whole year and in particular seasons (but again, not for their seasonality) (Table 2). Thus, in the principal plane (Figure 4), the first axis differentiates Andean species adapted to temperatures below 15 °C (*i.e.*, >2,000 m), on the left side from those growing below 2,000 m, on the right side. Characteristically, these rightmost species originate from the Amazonian and Orinoquian. The second axis separates the species according to precipitation. Thus *P. arbelaezii*, *P. costaricensis*,

P. chocoensis, *P. lobata*, *P. occidentalis*, *P. pacifica*, *P. palenquensis* and *P. tica* show preferences for high precipitation, a predominant condition in the Pacific region, and all are predicted to exist sympatrically. At the other extreme of the second axis, are species adapted to lower precipitation levels, specifically to the marked dry season of the Caribbean, such as *P. bicornis*, *P. serrulata*, *P. guazumaefolia* and *P. pallida*. Amazonian species take intermediate positions. The species repartition in the principal plane consistently reflects the potential for climatic adaptation of the groups that were defined for the analysis of altitudinal distribution. Thus, the *Tacsonia* group shows adaptation to cool conditions, while subgenus *Astrophea* and the *Passiflora*-like group show higher potential in hot and mild climates. The *Decaloba* group shows a much broader adaptation range, explaining its quite constant presence across the different biogeographic regions.

Figure 3. Distribution of total species richness (within circles) and species relative diversity in relation to altitude in Colombia, for genus *Passiflora* and five infrageneric groups.



3.4. Areas of Distribution and Endemism

Distribution parameters (MaxD and CA_{50}) have been given for each native species in Ocampo *et al.* [12]. Figure 5 shows a good correspondence between them, and their comparison provides information on species dispersion. For instance, a high MaxD and relatively low CA_{50} indicate low density, resulting from biological rarity and/or under-collection. The species with the widest distributions in Colombia (more than 1,100 km MaxD) are those showing a wide Neotropical distribution, such as the common *P. foetida*, *P. auriculata*, *P. quadrangularis*, *P. laurifolia*, *P. suberosa*, *P. serratodigitata*, *P. capsularis*, *P. rubra*, *P. misera*, and others of still considerable regional distribution, such as *P. vitifolia*, *P. coccinea*, *P. spinosa*, *P. nitida*, *P. subpeltata*, *P. maliformis*, *P. menispermifolia*, and *P. biflora*. Only *P. arborea* (Panamá to Ecuador) and

P. cumbalensis (Colombia to Peru) show a more restricted distribution. These high-MaxD species are concentrated at low to medium elevations, the only exception being *P. cumbalensis*. According to IUCN [58] criteria, they are not threatened (Least Concern category), except for *P. arborea* (Near Threatened; [12]). Between 200 and 1,100 km of MaxD, are species of regional importance, such as *P. mixta*, *P. ligularis*, and endemics with a relatively wide distribution, such as *P. sphaerocarpa* (96,244 km ²), *P. lehmanni* (91,156 km ²), *P. antioquiensis* and *P. mollis*. The latter displays a relatively high CA_{50} in its group, as its 17 observations are quite scattered along the Cordillera Occidental. The position of *P. coriacea* in this group of medium dispersion is surprising, as it is found in all Neotropical countries. The 71 species with MaxD values below 225 km include 34 narrow endemics, 21 of which are exclusive to nine departments, particularly Antioquia (six species), Tolima (four) and Santander (three). The 15 others show similar MaxD and CA_{50} but live across administrative divisions. Only four of these 36 narrow endemics are represented by 10 or more observations while 10 are only known from the type collection. The situation of 33 non-endemic species with a MaxD under 100 km must be examined in relation to their distribution in neighboring countries. *P. truxilliensis*, shared with Venezuela, is a narrow endemic living around the border. The distribution of 14 species extends to farther places in neighboring countries, and 18 species present a wide distribution, extending to non-neighboring countries. For example, *P. tricuspis* is only reported once, in the Andean foothill, so it has a null MaxD, however its distribution extends south to Bolivia. Sixteen of these 33 species are adapted to lowland conditions, which suggests that their apparent rarity is in fact due to the poor collecting in the corresponding regions.

Figure 4. Distribution of *Passiflora* species centroids in the PCA principal plane for climatic variables.

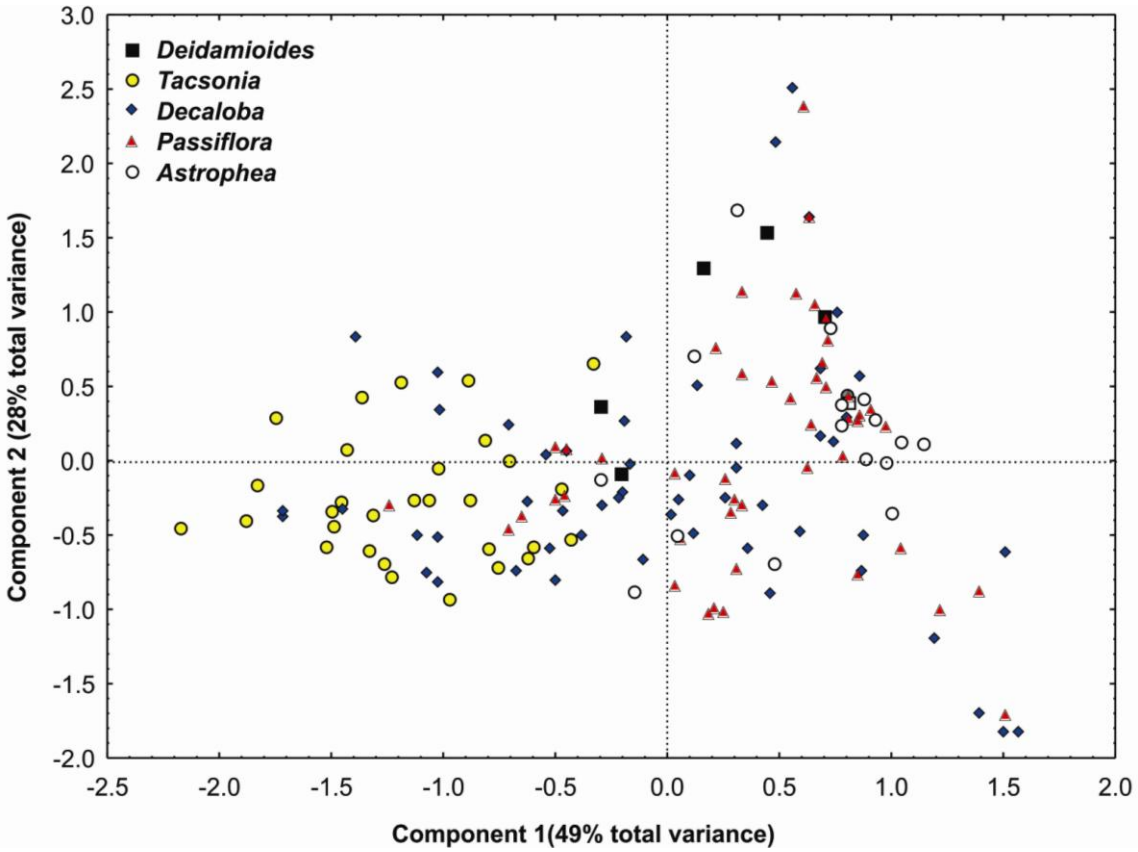
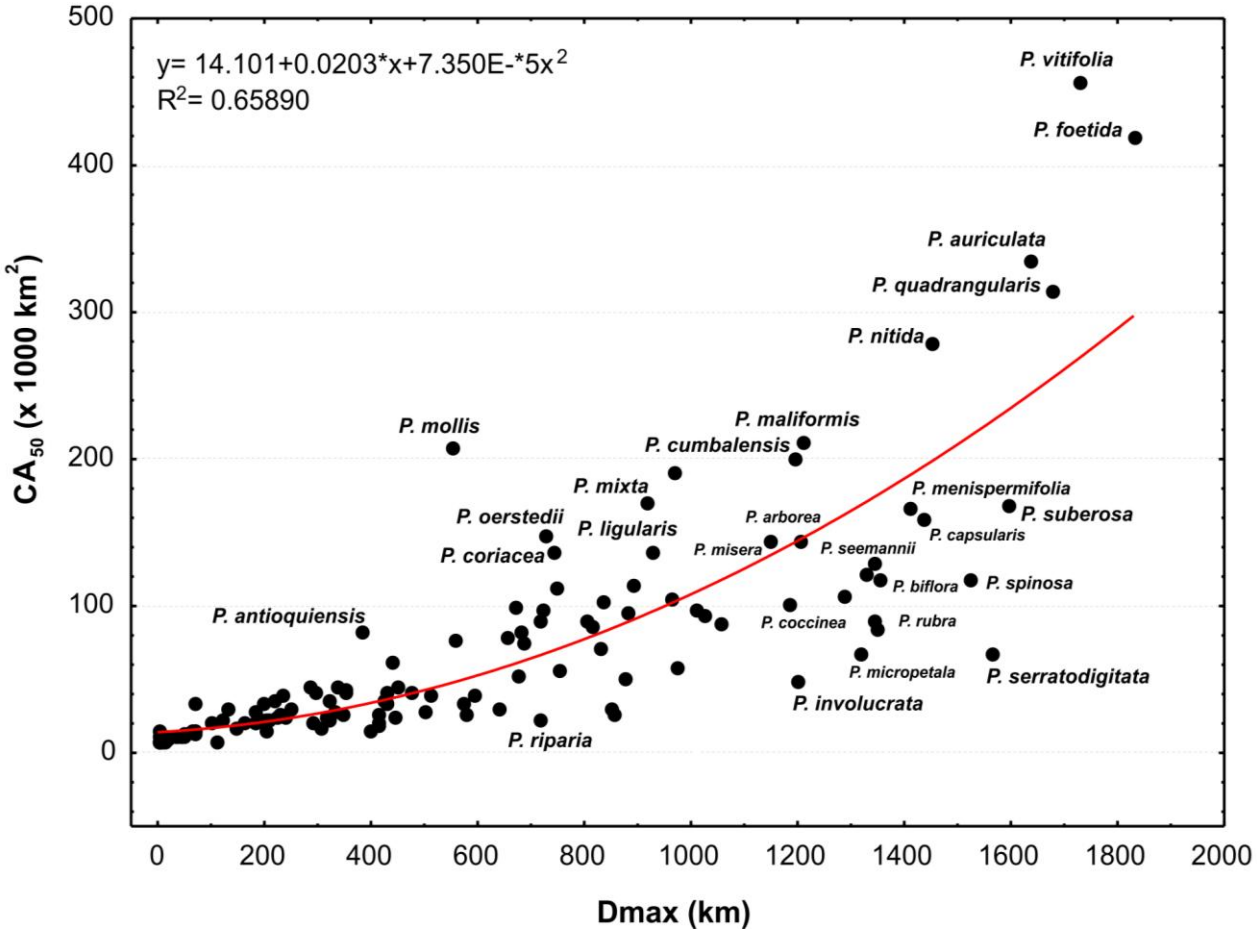


Figure 5. *Passiflora* species distributions in Colombia: circular area (CA_{50}) *vs.* maximum distance (MaxD).



3.5. Modeling Distributions and Species Assemblages

The predicted distributions of the 80 species with more than 10 observations cannot be presented here, but are available upon request. Figure 6 presents the potential distribution of richness obtained by assembling them. The areas of highest predicted richness (41 to 54 predicted sympatric species) are mostly located in the center of the country, on the slopes of the three cordilleras, between an elevation of 1,000 and 2,000 m. Despite collection intensity in these areas, the correspondence is not perfect between observed and modeled distribution. While the species-rich areas of Antioquia, Caldas, Quindío, Cundinamarca and eastern Boyacá, and even the poorly explored but promising Santander, are well represented on the map (areas 2, 5, 3, 4 and 1 respectively), only very small richness spots are drawn for Valle del Cauca (area 7), and none for Cauca and southern Huila. Conversely, predicted richness spots 6, 8 and 9 (eastern Tolima-northern Huila-southern Cundinamarca, western Caquetá, Nariño) were not detected in the analysis of observed diversity, suggesting collecting gaps. The model predicts a poor representation of *Passiflora* in the lowlands of the Caribbean, Orinoquian and part of the Pacific, as well as in the Sierra Nevada de Santa Marta, an isolated mountain range on the Caribbean Coast, reputed for its high level of endemism. In both cases, this may be attributed to the poor exploration of these areas (low densities of observations) and poor representation of their species (few observations/per species), resulting in them not having sufficient observations to be used in the

predictive modeling. This bias can be corrected by further collecting in these regions. Alternatively, materials of Colombian species collected in border regions of neighboring countries, belonging to the same biogeographic entities (e.g., the Venezuelan Llanos for the Orinoquian, Costa Rican and Ecuadorian Pacific, Brazilian, Ecuadorian and Peruvian Upper Amazonian) might be used to refine these models and increase the number of observations per species under analysis.

Table 2. Factor loadings, eigenvalues and percentages of variance for the first four components, resulting from the PCA analysis on 19 bioclimatic parameters for the 3,923 collection points.

Bioclim Parameters	**Principal components**			
	1	**2**	**3**	**4**
Annual Mean Temperature	**0.98**	0.17	0.09	−0.03
Mean Monthly Temperature Range	0.08	−0.21	−0.16	**−0.96**
Isothermality	0.00	0.06	**−0.95**	−0.01
Temperature Seasonality	0.45	0.03	**0.77**	−0.18
Max, Temperature of Warmest Month	**0.97**	0.16	0.12	−0.12
Min, Temperature of Coldest Month	**0.98**	0.20	0.06	0.04
Temp, Annual Range	0.08	−0.22	0.37	**−0.89**
Mean Temperature of Wettest Quarter	**0.98**	0.17	0.09	−0.02
Mean Temperature of Driest Quarter	**0.98**	0.18	0.10	−0.04
Mean Temperature of Warmest Quarter	**0.98**	0.17	0.11	−0.04
Mean Temperature of Coldest Quarter	**0.98**	0.17	0.07	−0.03
Annual Precipitation	0.24	**0.96**	0.04	0.10
Precipitation of Wettest Month	0.29	**0.91**	0.15	0.10
Precipitation of Driest Month	0.09	**0.91**	−0.28	0.13
Precipitation Seasonality	0.23	−0.55	0.60	0.00
Precipitation of Wettest Quarter	0.28	**0.91**	0.17	0.09
Precipitation of Driest Quarter	0.09	**0.93**	−0.25	0.13
Precipitation of Warmest Quarter	0.10	**0.87**	−0.20	0.12
Precipitation of Coldest Quarter	0.29	**0.89**	0.05	0.02
Eigenvalue	9.24	5.35	1.74	1.50
Percentage of variance	48.71	28.28	9.13	7.95

3.6. Conservation of Passiflora *species and their Habitat*

The biodiversity hotspot concept not only considers diversity but also endemism. Analyzing the distributions of New Zealand ferns, Mexican gymnosperms, or European butterflies, Lehmann *et al*. [36], Contreras-Medina and Luna-Vega [59], and Werner and Buszko [60] observed a poor correlation between both parameters. At the genus level, Jaramillo [61] found some correspondence between them for *Piper* diversity in the Chocó region, however there was a negative correlation between phylogenetic diversity and the proportion of endemics. For *Passiflora* in Colombia, we could not establish rigorously their correspondence, as the analysis was not designed for rare species, however we compared their spatial repartition, distinguishing four categories among the 56 endemics: those with a relatively wide distribution (MaxD > 100 km, 19 species), the narrow endemics

(11 species), the rare endemics (three species), and the rare narrow endemics (23 species). Six of the 11 narrow endemics, seven of the 23 rare narrow endemics, and none of the three rare endemics live in one of the areas defined by our analysis. Indeed, seven endemics are adapted to lowlands, and two belong to the Sierra Nevada de Santa Marta, an area of endemism not sufficiently taken into account for reasons explained previously. In any case, of the 37 living Andean rare/narrow endemics, only 13 live in one of the "hotspots". This proportion must be compared with more than 54 sympatric species out of 80 non-rare species whose distribution determined those hotspots. Thus, preserving these nine areas should have a less positive impact on the conservation of narrow endemics than on the general *Passiflora* diversity, which appears to limit the application of the biodiversity hotspot concept.

According to the analysis of complementarity for reserve selection, 52 sites of 25 × 25 km would suffice to represent all 162 native species throughout the country. The best five sites, in Caldas, Risaralda, Norte de Santander, southern Antioquia and Boyacá, capture a total 64 species. In just seven sites, 50 percent of all species could be conserved, though many of the endemic/rare species are not captured in these sites.

Figure 6 also shows a general lack of correspondence between the estimated distribution of *Passiflora* diversity and that of protected areas in the Colombian Andes, concentrated around the summits, obviously targeting páramo ecosystems. Very few small protected areas harbor a high *Passiflora* diversity: the watershed forest reserves of Sierra del Peligro (Boyacá, 16.5 km²), Río Nare (Antioquia, 118.8 km²), Río San Francisco, Cuchillas Peñas Blancas, and Cerro Quininí (Cundinamarca, 28.8, 16.3 and 18.0 km²). The Parque Nacional Farallones (Valle del Cauca) is the only reserve of national importance to protect part of a small *Passiflora* hotspot, on its eastern fringes. This poor coverage is not good news, neither for a genus including 71 percent threatened species, nor for the habitats where these species have developed numerous interactions with many other organisms.

Figure 7 shows a striking general superposition of areas of high *Passiflora* diversity on certain coffee growing zone ecotopes [62] whose conservation is of the utmost importance for Colombia. This is not surprising, as the corresponding elevation belts include or enclose those of major diversity. Clearly, efforts for the conservation of *Passiflora* habitats and genetic resources must be integrated in the more general management of the coffee growing zone environment at the landscape level.

Figure 6. Modeled distribution of Colombian *Passiflora* species diversity based on data from 80 species presenting more than 10 observations. Ellipses individualize high richness spots mentioned in the text. Distribution of protected areas in Colombia, showing poor correspondence with areas of high *Passiflora* diversity.

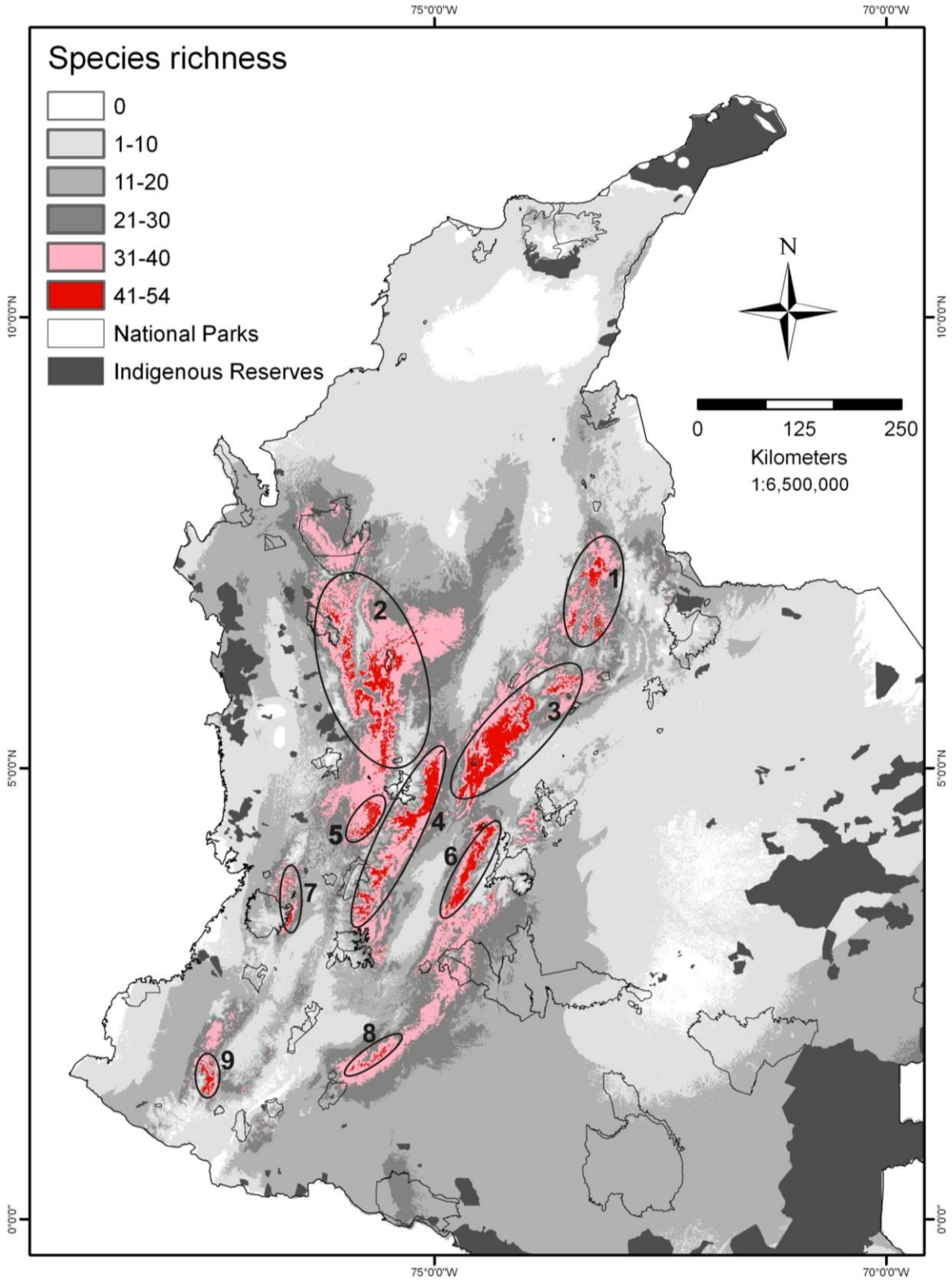
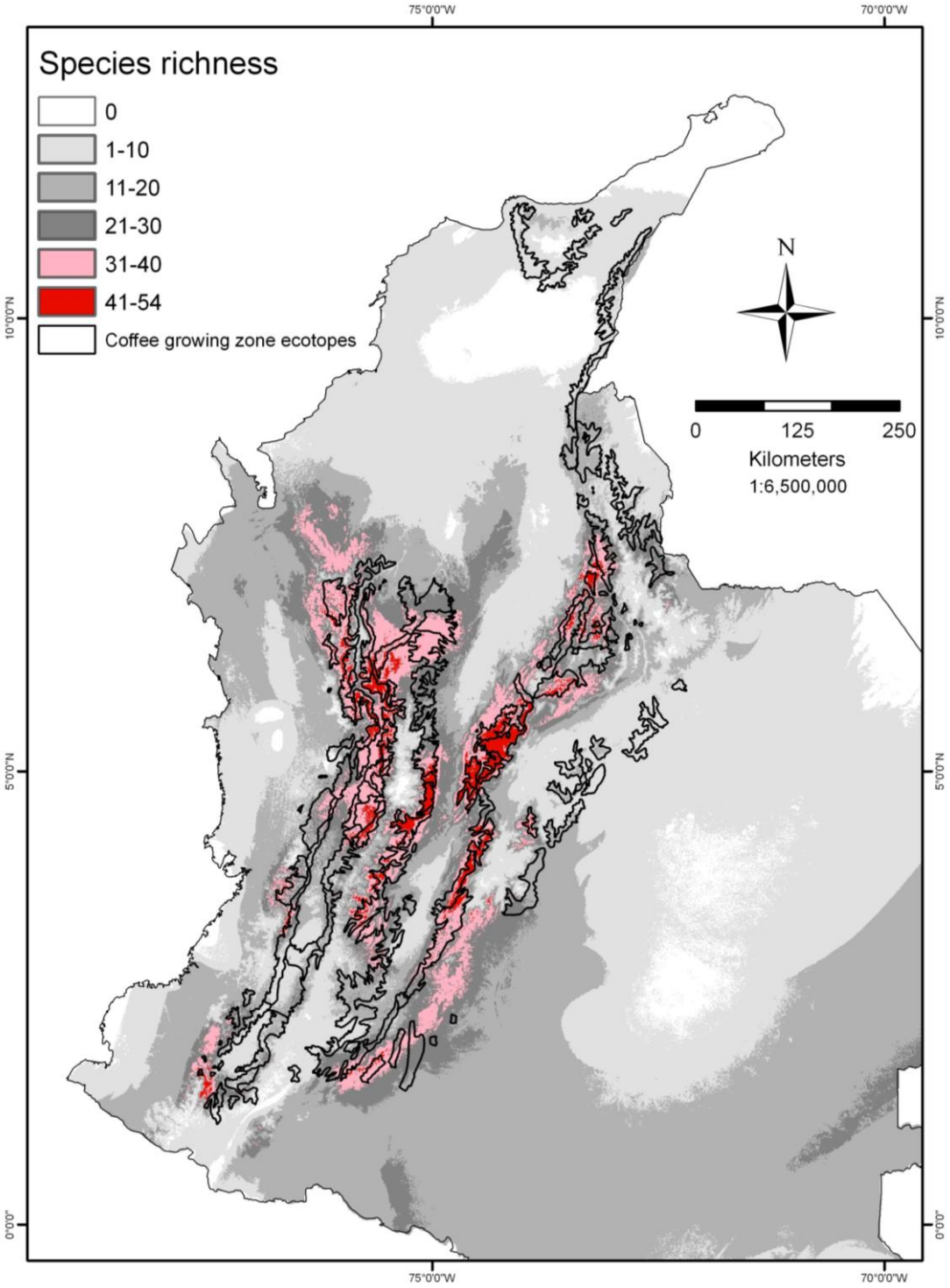


Figure 7. Correspondence between *Passiflora* species high richness spots and coffee growing zone ecotopes.



3.7. Passiflora *as Indicators of Biodiversity*

According to Pearson [34], an ideal indicator taxon should cumulate seven criteria: (i) a well-known and stable taxonomy, (ii) well-known natural history, (iii) readily surveyed and manipulated, (iv) higher taxa broadly distributed geographically and over a breadth of habitats, (v) lower taxa

specialized and sensitive to habitat changes, (vi) patterns of diversity reflected in other taxa, and (vii) potential economic importance. *Passiflora* clearly fills the fifth and seventh criteria, though we must keep in mind that several common species are indicators of more or less disturbed habitats. Concerning the fourth criterion, our analyses have repeatedly underlined that Colombian *Passiflora* species distribution is concentrated in the Andean region, so their use as indicators should be restricted to the corresponding elevation belts. Lianas growing in high trees are not always easily surveyed (third criterion), however their typical structures, showy flowers and interesting fruits make them easy to identify as a group, catching the attention of local populations and specialists, who can thus help localize the different species in particular places. The application of molecular techniques should produce important progress in the complex taxonomy of this group and further, in understanding its natural history. The sixth criterion is particularly important. The numerous interactions of *Passiflora* species with other organisms (surrounding vegetation, pollinators, and herbivores) constitute a first indication that their diversity is necessarily related to that of other ecosystem components. Another indication came from a preliminary study, where we found an excellent correspondence between the distributions of diversity of *Passiflora* and *Vasconcellea* (mountain papayas), another plant group whose diversification is clearly related to the rise of the Andes [38]. Similar results must be obtained with more plant taxa before considering unequivocally *Passiflora* as a reliable surrogate for floral diversity in Andean ecosystems. However, given the excellent correspondence between *Passiflora* diversity maps and coffee growing zone ecotope maps, we may already recommend them as useful indicators of habitat degradation or of restoration in this environmentally and economically very important region. They could complement other indicators working at the landscape level, such as birds, whereas insect diversity indicators work better at a smaller scale [63].

4. Conclusions

Collections of *Passiflora* have not been uniform as a consequence of difficulty of access and/or chronic social conflict in many areas. They have been much denser in the central coffee growing zone, Antioquia, Valle del Cauca and Cundinamarca. The southern and northeastern Andes, and the Caribbean have been little explored. For the lowland forests of the Pacific, the Orinoquian and the Amazonian, data are so poor that they are misleading. Despite the resulting sampling bias, collecting parameters clearly point to the concentration of observed *Passiflora* diversity in the Andes, and more particularly the central coffee growing zone.

The modeled species richness map allowed identifying nine richness spots of variable size, three of which, located in the southern and southeastern Andes of Colombia, correspond to collection gaps, as they were not detected in the analysis of observed diversity. Another probable collection gap, not detected by diversity modeling, corresponds to the Sierra Nevada de Santa Marta, an isolated mountain range with both high diversity and endemism. The proportion of endemics living in high richness spots is lower than the proportion of all species used for modeling, confirming the lack of relation between diversity concentration and endemism reported in other studies. If this is further substantiated in different groups of organisms, it could limit the application of the biodiversity hotspot concept, as the best-protected areas for diversity would not necessarily provide protection to a high proportion of narrow endemics.

Passiflora diversity is not conserved by the current network of Colombian protected areas. On the contrary, it is particularly concentrated on certain ecotopes of the coffee growing zone, *i.e.*, highly disturbed habitats, so any conservation effort must be integrated in local management strategies at the landscape level. *Passiflora* may provide an interesting indicator to evaluate the outcome of such efforts.

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Review

Origin and Domestication of Native Amazonian Crops

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Abstract: Molecular analyses are providing new elements to decipher the origin, domestication and dispersal of native Amazonian crops in an expanding archaeological context. Solid molecular data are available for manioc (*Manihot esculenta*), cacao (*Theobroma cacao*), pineapple (*Ananas comosus*), peach palm (*Bactris gasipaes*) and guaraná (*Paullinia cupana*), while hot peppers (*Capsicum* spp.), inga (*Inga edulis*), Brazil nut (*Bertholletia excelsa*) and cupuassu (*Theobroma grandiflorum*) are being studied. Emergent patterns include the relationships among domestication, antiquity (terminal Pleistocene to early Holocene), origin in the periphery, ample pre-Columbian dispersal and clear phylogeographic population structure for manioc, pineapple, peach palm and, perhaps, *Capsicum* peppers. Cacao represents the special case of an Amazonian species possibly brought into domestication in Mesoamerica, but close scrutiny of molecular data suggests that it may also have some incipiently domesticated populations in Amazonia. Another pattern includes the relationships among species with incipiently domesticated populations or very recently domesticated populations, rapid pre- or post-conquest dispersal and lack of phylogeographic population structure, e.g., Brazil nut, cupuassu and guaraná. These patterns contrast the peripheral origin of most species with domesticated

populations with the subsequent concentration of their genetic resources in the center of the basin, along the major white water rivers where high pre-conquest population densities developed. Additional molecular genetic analyses on these and other species will allow better examination of these processes and will enable us to relate them to other historical ecological patterns in Amazonia.

Keywords: molecular markers; genetic analysis; phylogeography; phylogenetics; crop dispersal

1. Introduction

At least 138 crops with some degree of domestication were being cultivated or managed by native Amazonians in various types of production systems at the time of European conquest, including 83 crops native to Amazonia and immediately adjacent areas in northern South America, and 55 exotic ones, *i.e.*, from other Neotropical regions, such as northeastern Brazil, the Caribbean and Mesoamerica [1]. Among the 52 crops with domesticated populations, 14 are fruit or nut trees or woody vines (27%); among the 41 crops with semi-domesticated populations, 35 are trees or woody vines (87%); and among the 45 crops with incipiently domesticated populations, all but one are fruit and nut trees. Overall, 68% of these Amazonian crops are trees or woody perennials. In landscapes largely characterized by forest, a predominance of tree crops is perhaps not surprising [1]. Nonetheless, the most important subsistence crop domesticated in Amazonia is an herbaceous shrub, manioc [2], and several other domesticates are also root or tuber crops, most of which are adapted to savanna-forest transitional ecotones with pronounced dry seasons.

Two types of domestication can be distinguished conceptually: landscape domestication and plant (or animal) population domestication [1]. Only the latter will be considered here because plant population domestication can now be examined with new genetic techniques, even though both sorts of domestication are of potential interest to historical ecology, since landscapes and the biota in them are profoundly affected, indeed molded by human actions. Additionally, these two kinds of domestication are intimately related because domesticated populations require some kind of landscape management, especially cultivation. Plant population domestication is a co-evolutionary process by which human selection on the phenotypes of promoted, managed or cultivated individual plants results in changes in the descendent population's phenotypes and genotypes that make them more useful to humans and better adapted to human management of the landscape [1]. The degree of change in populations can vary along a continuum from wild (the baseline, with no human-mediated change), through incipiently domesticated, to semi-domesticated, to domesticated. An incipiently domesticated population has gone through a founder event (defined as human selection of a small sample of the wild population and propagation of descendents from this sample; also called a bottleneck) that reduces its genotypic diversity and its phenotypic diversity varies only somewhat from the ancestral wild population in the traits selected by humans. A semi-domesticated population has gone through several sequential founder events that reduce further its genotypic diversity, but its phenotypic diversity is enhanced by accumulation of diverse alleles for traits selected by humans. Semi-domesticated populations tend to

have more ample geographic distributions than incipient domesticates, which may permit introgression with other wild, incipient or semi-domesticated populations of the same species; in turn, such introgression may offer additional alleles for selected traits, thus somewhat enhancing genetic diversity. The ample geographic distribution may include areas where wild populations do not exist, which reduces introgression of wild-type alleles and permits more rapid response to human selection. A domesticated population has been further selected for adaptation to human-modified landscapes, especially cultivated gardens and fields, and has lost its original ecological adaptations for survival without humans, especially its original dispersal mechanisms and survival capabilities [1]. Observe that domestication is a process that occurs at the population level, not the species level, so that it is incorrect to affirm that species X is a domesticate, unless all wild populations have become extinct, which is an uncommon occurrence; it is most generally correct to affirm that species X exhibits domesticated populations. Exceptions to this generalization exist, for example, when the end-result of the domestication process is a new species; a particular case of the latter is interspecific hybridization followed by chromosome doubling, resulting in the formation of allopolyploids [3], as in guaraná, discussed below. An aside is worth adding here: the term "proto-domesticate" is often used, but *protós* is Greek for "first", leading to definitions such as 'original' and 'primitive' (as in "first order"); since domestication is a process and the domesticated population is the result, the domesticate is not primitive, but derived. Hence, the term should be avoided.

The degree of modification during domestication can be dramatic in many crops, including some tree crops, such as peach palm, where the difference in fruit size between the wild type and the most derived domesticated population is on the order of 2000% [4]. Several other Amazonian tree crops show considerable, although not as dramatic, modification due to domestication [5]. Given the long generations and typically outcrossing reproductive systems, these degrees of change suggest that domestication started quite early, perhaps at the beginning of the Holocene, rather than when production systems coalesced and became prominent 3,000 to 4,000 years before present (BP). The archaeological record, however, does not contain early records of Amazonian tree crops, although manioc and sweet potato were present between 8,000 and 6,000 BP in caves along the western Andean foothills of Peru [6], indicating that they were domesticated earlier. The earliest lowland tree crop, guava, was present in the same area before 5,000 BP [6]. The archaeological record of lowland South America east of the Andes is much less studied than the dry Pacific coast, western foothills and the highlands, where preservation is better, but is gradually gaining attention and patterns will become apparent as critical mass increases.

Better ethnographic and historical information exists for more recent periods. The crops in Amazonia at conquest were distributed in numerous centers, regions and micro-centers of crop genetic diversity, located principally where Native Amazonian populations were most abundant [7], *i.e.*, along the principal white water rivers, but also in the upper Negro River, which was and still is a major center of Amazonian ethnic and linguistic diversity. Some tree crops, such as Brazil nut, are quite long-lived (500 to 1,000 years), so that their pre-conquest distribution can be mapped from their modern distribution. Balée [8] used this type of information to estimate the proportion of the Amazon basin that had been modified by pre-conquest human activity (nearly 12%). Unfortunately, few species permit this type of analysis, but living plants can provide other information that permits inferences

about their origin, domestication and dispersal before and since European conquest. This information is in their DNA and is accessed with different molecular techniques.

There are numerous types of molecular markers used in genetic analysis, each with advantages and disadvantages, as well as different information contents [9]. In plants, both nuclear DNA (diploid) and chloroplast DNA (haploid) offer important and somewhat different information, with nuclear DNA subject to rapid change via recombination and chloroplast DNA subject to less rapid change; the latter is generally maternally inherited, which makes it especially useful for some kinds of analyses, such as distinguishing seed dispersal from pollen dispersal. So called dominant markers are cheaply and easily generated, but are less informative because they do not distinguish between homozygotes and heterozygotes at a particular DNA locus; the primary marker cited here is Random Amplified Polymorphic DNA—RAPDs, which are generated principally from nuclear DNA. Co-dominant markers are often more expensive to generate, but are more informative because they distinguish homozygotes and heterozygotes; examples are protein polymorphisms, especially in enzymes, Simple Sequence Repeats—SSRs (also called microsatellites), and Restriction Fragment Length Polymorphisms—RFLPs; the latter two can be either nuclear or chloroplast. Direct sequencing of specific regions of DNA is becoming the most important strategy to study genetic variability as the cost falls continually; it is also the most informative. Sequence polymorphisms include insertions and deletions of base pairs or sections of DNA, as well as substitutions in nucleotide sequences, such as Single Nucleotide Polymorphisms—SNPs. Ideally molecular markers should be selectively neutral, that is they should not be under selective pressures so that they do not reflect different local adaptations to natural or human selection.

New research with these molecular tools attempts to identify origins and possible dispersals via the patterns of genetic diversity in living populations of native Amazonian crops, a field of study known as phylogeography [9]. Phylogeography is the analysis of the geographic distribution of genetic variants, especially lineages of genes, which is generally due to dispersal of organisms (seed dispersal in plants) and thus provides insight into the history of a species. The same information permits inferences about the domestication process [10-12] and can even be used to estimate the approximate age of the founder events, although this has yet to be attempted with an Amazonian crop. This contribution reviews recent molecular studies of a set of native Amazonian crops, some important, others less so, and identifies emergent patterns that can be used to interpret crop domestication and dispersal before conquest.

2. The Crops

We will review the recent molecular genetic literature on only nine of the 83 native Amazonian crops, principally because the number of crops examined is still quite small. Manioc is the most important subsistence food crop domesticated in Amazonia and was one of the first studied with molecular techniques. Cacao is arguably as important, although chocolate lovers might place it first. Peach palm is the premier Neotropical tree fruit-crop and has recently been the focus of considerable research. The *Capsicum* peppers are certainly the most important Neotropical spices and at least one species appears to contain domesticated populations of Amazonian origin. Pineapple is often considered the queen of fruits and is certainly the most important fruit crop from Amazonia. Inga is a legume tree crop often called ice cream bean because of the edible aril around the large seeds; it is

currently an important agroforestry species, used principally for green manure and shade for other crops. Guaraná is a stimulant that is gaining worldwide popularity, although its principal use in Brazil is to flavor soft drinks. Brazil nut is the emblematic Amazonian tree, whose edible seed is recognized around the world. Cupuassu is a cacao relative whose pulp is used for making fruit juices and other products.

Manioc, peach palm, *Capsicum*, pineapple, inga and guaraná all have domesticated populations, while cacao has semi-domesticated populations, and Brazil nut and cupuassu have incipiently domesticated populations [1]. Eight of the nine are outcrossing species, the exception being *Capsicum*, and two are generally vegetatively propagated (manioc and pineapple). The available information concerning these nine species is not uniform, as much remains to be done. Nonetheless, the information now available and reviewed here provides fascinating insights into the origin and domestication of native Amazonian crops, placing Amazonia squarely in the list of important centers of crop genetic diversity.

2.1. Manioc

Manioc (*Manihot esculenta* Crantz, Euphorbiaceae) is the most important food crop that originated in Amazonia and is grown throughout the tropics; it is the sixth major food crop produced globally. The term manioc is derived from the Tupi word *maniot*, while the term cassava comes from the Arawak words *cassavi* or *cazabi*, meaning bread [13]. Although some modern cultivars derive from modern breeding efforts and market demand, manioc is mostly cultivated by traditional farmers with few or no inputs or mechanization. Nonetheless, manioc is extremely important to the food security of an enormous number of smallholders in tropical countries and is the main carbohydrate resource for about 800 million people.

The origin of manioc as a crop has long been debated. The genus *Manihot* has 98 species distributed throughout the Neotropics from Mexico to northern Argentina [14]. Two centers of diversity are recognized: one in Brazil with about 80 species; one in Mexico with 17 species. A taxonomic classification based only on phenotypic variation is unreliable because of considerable trait overlap. For a long time, manioc was considered a cultigen (without a wild conspecific ancestral population) and was thought to have originated from a series of introgression events among wild species [14]. Based on phenotypic similarities, *M. aesculifolia*, which occurs in Mesoamerica, was thought to be one of these wild relatives [14]. Later, another Mesoamerican species, *M. carthaginensis*, was proposed as a wild relative [15,16]. Early studies with molecular markers did not clearly resolve the phylogeny of the genus [17,18]. However, they did identify a clear separation between the Mesoamerican and South American lineages, and found that cultivated manioc always grouped with South American species, suggesting that the crop was domesticated in South America. The great phenotypic variation and the low-resolution phylogenies also suggest that the genus *Manihot* experienced a recent period of super-diversification.

The taxonomy of *Manihot* was elucidated in the mid-1990s. Based on phenotypic traits, Allem [19] proposed that manioc consists of three subspecies: *Manihot esculenta* ssp. *esculenta* (cultivated form), *M. esculenta* ssp. *flabellifolia* (the closest wild relative) and *M. esculenta* ssp. *peruviana* (probably not involved in manioc domestication). Together with *Manihot pruinosa*, these form the primary gene pool

of manioc. Allem also speculated that manioc was domesticated somewhere on the Central Brazilian Plateau, the main center of diversity in South America, where 53 *Manihot* species occur.

Three different molecular markers [sequencing of the nuclear gene glyceraldehyde 3-phosphate dehydrogenese (G3*pdh*), SNPs and SSRs] were used to evaluate the relationships among cultivated varieties of manioc and wild populations of *M. esculenta* ssp. *flabellifolia* and *M. pruinosa*. It was determined that the latter species does not contribute to the gene pool of cultivated manioc and that the genetic variability found in cultivated manioc is a subset of the genetic variability found in the populations of *M. esculenta* ssp. *flabellifolia* that occur in southwestern Amazonia [2,20,21]. Recently Léotard *et al*. [22] used the G3*pdh* gene to examine cultivated manioc, a wider geographic sample of *M. esculenta* ssp. *flabellifolia* and other potentially hybridizing *Manihot* species, and validated Olsen and Schaal's results [2,20,21], strongly suggesting that manioc was domesticated only once from *M. esculenta* ssp. *flabellifolia* populations occurring in northern Mato Grosso, Rondônia and Acre states, in Brazil, and adjacent areas of northern Bolivia. Domestication must have started before 8,000 BP, as that is the earliest date reported from the Zana and Ñanchoc valleys of coastal Peru [6].

The domestication of manioc resulted in significant changes in *M. esculenta* ssp. *flabellifolia*, the most important being the development of tuber roots capable of storing large amounts of carbohydrates. After its initial domestication, different selective pressures gave rise to two major groups of varieties: "sweet" manioc and "bitter" manioc [23,24]. This separation is based on the cyanogenic potential of the roots, which accumulate linamarin and lotaustralin, substances that are hydrolyzed to cyanide when the root cortex tissues are damaged. Sweet varieties have low amounts of cyanogenic glycosides (<50 ppm fresh weight) and can be safely consumed with simple processing (cooking or sometimes even raw). On the other hand, bitter varieties have large amounts of cyanogenic glycosides (>50 ppm fresh weight) and demand considerable detoxification and processing before consumption in the form of flour (*farinha*, *farine*), flat breads (*beiju*), cassava bread or fermented drinks. Although this classification is dichotomist, continuous variation among manioc varieties and related wild species is observed, suggesting that sweet and bitter manioc are the outcome of independent selections from an ancestor with intermediate toxicity [25].

In contrast to what is observed in most domesticated crops, there is strong selection for manioc varieties with high toxicity, especially in Amazonia where the majority of varieties are bitter. Some studies identify a tendency for higher yield in bitter varieties than in sweet ones, which may be due to the greater pest and pathogen resistance of bitter manioc varieties [26,27]. In Tukanoan settlements in northwestern Amazonia the selection of varieties appears to be due mainly to the foods that can be prepared from them and bitter manioc can be used to prepare more kinds of food [28].

In general, bitter manioc cultivation is associated with the courses of the major Amazonian rivers, as well as the coastal areas of South America, where population densities were highest before conquest. On the other hand, sweet manioc is the main crop throughout the headwaters of these same rivers in western Amazonia, including the whole length of the Ucayali and Marañon Rivers in Peru, the southern periphery and up into Mesoamerica. It is also commonly grown on a minor scale where bitter manioc is the major crop [25]. These patterns may be due to the costs and benefits of toxicity, with greater benefits of toxicity for large sedentary populations with semi-permanent fields, because these attract greater pest and pathogen pressure, and with greater costs for small, more mobile

populations [25]. While these ideas may explain pre-conquest distributions, it is not clear if they explain current distributions of bitter and sweet.

Although ease of vegetative propagation is another outcome of domestication, manioc has not lost its capacity for sexual reproduction, which plays a very important role in the evolutionary dynamics of the crop. Once produced, seeds become part of the soil seed bank, and seedlings sprout among the vegetatively propagated varieties in the plots [25,29-31]. Many smallholders let these volunteers grow, either unconsciously or consciously [32,33]. At the time of harvest, they decide if a given volunteer is worth including among the plants that will be vegetatively propagated [25,32,34,35]. If so, smallholders can either incorporate the seedlings into an existing variety or use them to establish a new variety [25,29,31,36,37]. Genetic analyses confirmed seedling incorporation by detecting high polymorphism in local varieties [24,31,36,38], and by demonstrating that local varieties are polyclonal, with one predominant clone and a set of morphologically similar plants that are genetically different [30,34,39].

2.2. Cacao

Cacao (*Theobroma cacao* L., Malvaceae) is native to Amazonia, but is generally believed to have been domesticated in Mesoamerica [40], since this is the only region in which evidence of cultivation existed at the time of European conquest [41]. The name *Theobroma,* or "food of the gods," was coined by Linnaeus to honor the Aztecan belief in the divine origin of cacao, although he might not have chosen it if he had experimented with the Aztecan beverage made with a mixture of fermented and ground cacao seeds, maize and *Capsicum* peppers. The specific name *cacao* and the term *chocolate* are corruptions from Nahuatl, the Aztec language. The chocolate that we are all familiar with is a European invention, made with vanilla and sugar, and much easier to accept as a "food of the gods" than that made with maize and chili peppers. Although the Maya have been credited with its domestication, the name for cacao can be reconstructed in proto-Zapotecan, a language spoken in southern Mexico by about 3,350 BP, while proto-Mayan is dated to about 2,400 BP [42], strongly supporting a much earlier dispersal.

Until recently there were three hypotheses about the relationships among cultivated cacao in Mesoamerica and wild cacao in Amazonia [40]: a south to north dispersal; a north to south dispersal; and *in situ* development of types with no early dispersal. These hypotheses attempt to explain the differences between the Criollo types (subsp. *cacao*; [43]) found from northwestern South America to Mesoamerica and the Forastero types (subsp. *sphaerocarpum*) found in Amazonia and northeastern South America, while accepting the observation that cacao grows wild from southern Mexico to the southern edges of Amazonia. However, cacao survives easily in appropriate humid forest ecosystems when abandoned, which led Clement [1] to classify it as a crop with semi-domesticated populations, rather than with fully domesticated populations.

Using two co-dominant markers (RFLPs and SSRs), and controlling sample origin very carefully to distinguish between materials that were less likely to have been genetically contaminated by the last five centuries of germplasm exchange, Motamayor & Lanaud [44] show clearly that Criollo types are derived from South America, as had been hypothesized by Cheesman [45], who identified the center of origin in the upper Napo, Putumayo and Caquetá River basins adjacent to the Ecuadorian and

Colombian Andes. Motamayor and Lanaud suggest that northwestern Venezuela may be important because there are very early reports of a chocolate-like beverage called *chorote*, religious use and extraction of seed fat all based on genetically Criollo type cacao. These early reports should be interpreted with caution, however, as they may already reflect European influences [41], rather than purely native developments, and no archaeological records of cacao exist in the region [44]. There are also no reports of cultivation in this area until much later [41].

One of the major implications of this study is that Cuatrecasas' [43] classification of two subspecies is incorrect [44], which also raises questions about the usefulness of the Criollo-Forastero dichotomy, even though numerous molecular genetic analyses have identified clear differences between these types (references in [44,46]). These conclusions led to a search for a new intraspecific classification that would be useful for plant breeders [46]. With a very large data set (1,241 plants; 96 SSR), the Structure program [47] was used to identify genetic groups with no *a priori* hypotheses, which also allowed identification of genebank errors and their elimination [46].

Instead of the two traditional groups (Criollo and Forastero) and their hybrid (Trinitario), ten genetically different clusters are strongly supported by Structure and various other analyses [46]. The greatest diversity is found in western Amazonia (7 groups, including Nacional). Three groups are especially important to our discussion: Criollo, Nacional and Amelonado. These groups have been classified as traditional cultivars [46], which suggests some degree of domestication. The Criollo traditional cultivar is found in northwestern Ecuador, northwestern Venezuela (around Maracaibo), northern and western Colombia, and throughout Central America to southern Mexico, including the Maya heartland. The Nacional is a western Ecuadorian cultivar, with close affinity to several populations in extreme northern Amazonian Peru and the Curaray group in Amazonian Ecuador. The Criollo, Nacional and Curaray groups occupy one major branch of the Neighbor Joining dendrogram, suggesting an Ecuadorian Amazonian origin for both traditional cultivars. The Amelonado occurs in the lower Amazon basin and has less morphological variation than other Amazonian cacaos, especially with respect to fruit characteristics [40]. The Amelonado groups with the French Guiana group, suggesting a possible eastern Amazonian origin for this traditional cultivar. Close scrutiny of the molecular information shows that these three traditional cultivars have low numbers of private alleles (alleles that occur in only one group), while the western Amazonian groups generally have high numbers, with one or two exceptions that may be due to sampling [46]. One way to explain these low numbers is that they represent the genetic bottlenecks that accompany continued selection by humans, which is never doubted for Criollos.

Note also that the Criollo and Amelonado traditional cultivars are at the northwestern and eastern extremes of cacao distribution in the Americas. The discussion of Criollos has always included human-mediated dispersal, although clear records of cultivation appear only in the northern half of its range, from Costa Rica to Mexico [41]. The early chronicles from eastern Amazonia do not report cultivation. However, Patiño [41] cites Jacques Huber [48], who refers to the lack of cacao east of Obidos and Santarém and west of Marajó Island. Patiño [41, p. 351] concludes that the cacao in eastern Pará is probably the result of "ancient cultivation." Ethnographic observations in French Guiana also suggest that cacao has long been cultivated in the region by native peoples [49]. While both Huber's and Barrau's observations are much too late to offer assurance that cacao was cultivated before conquest, the relative uniformity of Amelonado fruits and the low number of private alleles

suggest that this traditional cultivar may have been at least incipiently domesticated in eastern Amazonia.

It is appropriate to ask why only Criollos are generally considered to be at least semi-domesticated, whereas even the traditional cultivars Nacional and Amelonado are not. It may be that cacao researchers have been blinded by the name "food of the gods." In other words, if Native Americans did not make chocolate, then they did not domesticate cacao. Considering that numerous other Amazonian fruits with sweet juicy pulps contain domesticated populations [1], such as abiu (*Pouteria caimito*), biribá (*Rollinia mucosa*), mapati (*Pourouma cecropiifolia*), sapota (*Quararibea cordata*), it is possible that cacao could have been selected initially for its pulp. In fact, this is probably the only way to get cacao from Amazonian Ecuador (the Curaray group) over the Andes into western Ecuador (the Nacional traditional cultivar), then up the Colombian Pacific and around to Maracaibo, before or simultaneously going north into Panama and Costa Rica. Remember that there were no reports of cultivation in any of these areas, nor any reports of chocolate, except the *chorote* in northwestern Venezuela.

Any sweet fruit can be fermented to obtain a mildly alcoholic beverage. Recent chemical archaeology shows that several types of pottery vessels found in Honduras, part of the Mayan heart-land, contain theobromine, a chemical compound found in *Theobroma* spp. The earlier vessels have shapes that suggest they were used to serve a fermented beverage, while the later vessels have shapes characteristic of those used with frothed chocolate [50]. Interestingly, the earlier vessels date to 3500 BP, in close agreement with the appearance of the word for cacao in proto-Zapotecan by 3350 BP [42]. The authors suggest that the first uses for cacao in Mesoamerica were similar to those in South America—the sweet pulp around the seed was consumed directly or fermented—and only later did the fermented seed itself become an additional part of the beverage, finally becoming the "food of the gods." While there are no reports of the cacao pulp beverage in South America, numerous other fermented beverages made from sweet or starchy fruits and roots are mentioned [41].

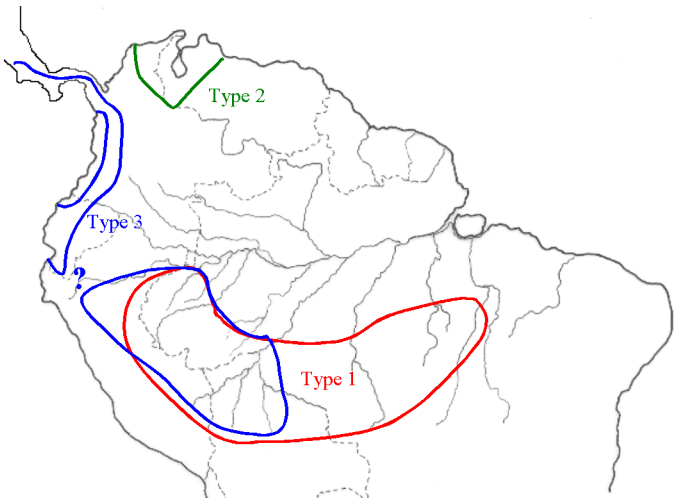
For domestication to occur, there must be human selection and propagation, both of which can be either intentional or unconscious [1,51]. Most domestication events were surely initially unconscious and cacao is an ideal example of how this might have occurred. Some variation in fruit pulp sweetness and juiciness exists in any natural cacao population, and humans who collected cacao to suck on the pulp would soon learn which trees offered the best fruit. These trees would be preferred for harvesting a sack of fruit to take back to camp or along a trek into another river basin. At camp, discarded seeds would germinate immediately and grow to reproductive age if environmental conditions were appropriate; if they germinated and grew in dump heaps they would even be less dependent on environmental conditions because of extra nutrients and light [52]. These new populations around camps would be more homogeneous than the source populations, but would certainly contain progenies from numerous seed trees, allowing for crossing among selected types, which in turn would yield sweeter and juicier pulps in the next generation. If this occurred in Amazonian Ecuador or in French Guiana, cacao could be rapidly dispersed over the Andes or into the estuary of the Amazon River, respectively, without any cultivation, but with selection and propagation. Further genetic analysis can certainly shed more light on this hypothesis.

2.3. Peach Palm

The peach palm (*Bactris gasipaes* Kunth, Arecaceae) is the only Neotropical palm with domesticated populations [4]. It may have been selected initially for its wood, preferred for tool making, and later for its abundant oily fruits, and finally for starchiness in the fruits, making them good for fermentation [53]. Peach palm is currently an agribusiness for its hearts-of-palm. The species presents considerable morphological and genetic variability in its wild and cultivated populations, due to adaptation to different environments and different stages of domestication, respectively. Thousands of years of domestication have resulted in landraces, each of which has common morphological, chemical and productive characteristics due to a common genetic origin [54]. These landraces are widely distributed in the humid Neotropics, especially Amazonia.

Throughout the 20th century, peach palm was considered a cultigen, with no wild conspecific ancestor. The revision of *Bactris* [55] gathered all cultivated populations of peach palm into var. *gasipaes* and all wild populations (previously identified as species) into var. *chichagui* (H. Karsten) Henderson. Within var. *chichagui* three types were proposed, with little description of their fruits and without detailing their distributions, which was done later by others [56] (Figure 1). Nonetheless, this revision now permits phylogenetic hypotheses that can be tested with genetic tools.

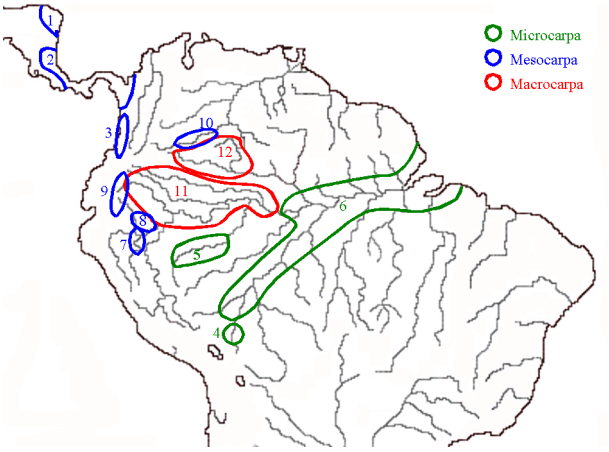
Figure 1. Distribution of the three wild types of *Bactris gasiapes* var. *chichagui* [56].



There is considerable speculation about the origin of the founder event(s) that lead to domesticated peach palm populations, with three hypotheses currently under consideration: (1) a single domestication event in southwestern Amazonia [57], with some morphological [58] and molecular (RAPDs, a dominant marker; [59]) evidence, and the occurrence of two wild types (1,3); (2) a single domestication event in northwestern South America, with archaeological coincidences [60] and the occurrence of a wild type (3); and (3) multiple domestication events in the distribution of two wild types (1,3), with coincidences in common SSR allele frequencies between var. *chichagui* and var. *gasipaes* in some localities [61,62]. Determining the correct hypothesis will require analysis of the landrace complex and its relationships with the various populations of the three wild types, a complex task given introgression between domesticated and wild populations [63].

Some of the landraces have been characterized morphologically and mapped [64]. The identification and classification of Amazonian landraces was based on morphometric characterization and multivariate analyses using a descriptor list designed for *in situ* and *ex situ* use. A hierarchical classification based on fruit size was proposed [64], with microcarpa landraces having small fruit (<20 g; Pará, Juruá and Tembe), mesocarpa landraces having intermediate sized fruits (20–70 g; Pampa Hermosa, Tigre, Pastaza, Solimões, Inirida, Cauca, Tuira, Utilis, Guatuso and Rama), and macrocarpa landraces having large fruits (>70 g; Putumayo and Vaupés) (Figure 2). The size of the fruit reflects the degree of modification due to human selection during the domestication of peach palm [57].

Figure 2. Geographical distribution of landraces of *Bactris gasipaes* var. *gasipaes*: 1. Rama, 2. Utilis (including Guatuso and Tuira), 3. Cauca, 4. Tembé, 5. Juruá, 6. Pará, 7. Pampa Hermosa, 8. Tigre, 9. Pastaza, 10. Inirida, 11. Putumayo (including Solimões), 12. Vaupés [after Rodrigues *et al*. [59], with modifications].



Several genetic studies have been conducted over the last decade to understand the great genetic variability within and among landraces. The first study used isoenzymes (co-dominant markers) and found that the Pará landrace of eastern Amazonia grouped with the Tembé population of northern Bolivia (once designated *Guilielma insignis* Martius [55]), while the other landraces grouped on another branch of the dendrogram [65]. The authors proposed geneflow along the Madeira River to account for this grouping, as well as geneflow through western Amazonia to Central America.

Dominant RAPD markers have been used extensively by the Brazilian group to validate many of the landraces in the genebank. One study concluded that the Pará, Putumayo, Pampa Hermosa and Utilis landraces are valid, while there is only one landrace in Central America rather than three and the Solimões landrace is part of the Putumayo landrace in western Amazonia [59]. This study also observed that the Utilis landrace had lower polymorphism and heterozygosity than the Amazonian landraces. The dendrogram using Nei's [66] genetic distances grouped the Pará landrace with a sample of var. *chichagui* type 1 from Acre, Brazil, and the Putumayo, Pampa Hermosa and Utilis landraces, with a sample of var. *chichagui* type 3 from western Amazonas, Brazil, in the other group. Their dendrogram was very similar to that of Rojas Vargas *et al*. [65], although with more landraces and populations. They proposed the most parsimonious hypothesis: a single domestication event in southwestern Amazonia, with two dispersals, one to the northeast and another to the northwest. A

second study used the same RAPD markers, the same landraces, as well as samples of the Juruá, Cauca and Vaupés landraces, and samples of var. *chichagui* type 1 from the Xingu River, Brazil, and type 2 from the Magdalena River, Colombia [67]. This study confirmed the previous validation [59] and the separation of the Pará landrace from the others, as well as validating the Juruá landrace and eliminating the two wild populations as parents of domestication events. A third study with the same markers, landraces and additional populations [68] revalidated the landrace complex, confirmed the Pará landrace as having affinities with the upper Madeira River, and further confirmed the Western Amazonian complex as separate from the southeastern complex. The third study also designed a core collection within the Brazilian genebank to stimulate further morphological characterization, permit duplication and facilitate future analysis of the phylogeography and phylogenetics of *Bactris gasipaes*.

During the last decade, numerous microsatellite primers were developed and tested [69-71]. Four of the first set were used to examine relationships among seven wild and eleven cultivated populations [62]. They detected considerable introgression among adjacent wild and cultivated populations, as expected following the study in Ecuador [63]. Unfortunately, they did not analyze the cultivated and wild populations separately, and created a Neighbor Joining dendrogram from Nei's minimum genetic distance, which they interpreted as showing three domestication events, even though the dendrogram's topology was not much different from the first RAPD study [59]. They also excluded the Pampa Hermosa landrace from the final dendrogram, although it was part of their preliminary study [72], which found a topology even more similar to the first RAPD study. Although quite intriguing, the small number of microsatellites does not permit much precision.

After a decade of study, the origin of the cultivated peach palm is still speculative, principally because of the numbers and types of markers used. A new study [73] with 17 microsatellite loci examined the phylogeography of the landrace complex represented in the newly created core collection [68], which has 40 accessions. This phylogeographic analysis used the Structure program to revalidate landraces and Nei's [66] genetic distance to create a Neighbor Joining dendrogram, which was quite similar to the first and subsequent RAPD dendrograms [59,67,68], as well as the first microsatellite dendrogram [72]. Relationships with two var. *chichagui* types suggest considerable introgression.

Universal chloroplast DNA sequences [74] are now being used to determine the phylogenetic relationships among cultivated and wild populations in the core collection, as well as the closely related *B. riparia* and the more distantly related *B. simplicifrons*, both used as outgroups. Because the chloroplast genome is generally maternally inherited, these sequences should identify one or a few haplotypes within the landrace complex, one or two of which may also occur in var. *chichagui*, which would pinpoint the wild populations involved in the domestication of the landraces, as was done with manioc [20]. The first results using these cpDNA sequences showed that one of the cultivated landraces, Pará, has chloroplast haplotypes different from the other cultivated and wild populations (Cristo-Araújo *et al*., Unpublished), suggesting that peach palm was domesticated more than once, as hypothesized by Mora Urpí [61], although southwestern Amazonia still seems to be the primary region of origin, as hypothesized by Rodrigues *et al*. [59].

2.4. Capsicum Peppers

The genus *Capsicum* (Solanaceae) undoubtedly originated in the Americas [75], although one species is named *C. chinense*, suggesting an Asian origin; in fact, *C. chinense* is the most Amazonian of the *Capsicum* peppers [76,77]. The earliest record of pepper use is from archaeological excavations in the Valley of Tehuacán, Mexico, and date from about 8,500 BP [78]. Starch derived from chili peppers and preserved on artifacts from seven archaeological sites ranging from the Bahamas to Andean South America appeared by 6,000 BP [79]. The peppers were present from the north of Chile and Argentina to northern Mexico and the southern United States at the time of European conquest [76,77]. Today they are distributed worldwide and grown for use as spices, vegetables, ornamental plants and medicine, in temperate and tropical areas [76].

Several criteria are used to determine more precisely where a domesticated population originated and in which directions it was dispersed: The crop must have been domesticated somewhere in the range of its wild relatives, the center of diversity may indicate the center of domestication of the crop, and archaeological, historical and linguistic data can provide evidence [80,81]. The prehistoric dispersals of wild peppers were probably due to birds before humans became important dispersal agents [82]. Different species of *Capsicum* were domesticated independently in several regions of the Americas [10,83]. Three regions are considered to have been independent areas of *Capsicum* domestication: Mesoamerica, the Andean region and the tropical lowlands of South America [10]. In each area of origin, one or more species was brought into domestication, perhaps intentionally, perhaps not, and they were then dispersed to different areas where they continued to be selected, resulting in distinct morphological types. Domestication resulted in changes, especially in the fruits. The fruits of the wild types are small, erect, red and deciduous, while fruits of domesticates are larger, often pendent, not deciduous and varied in color. Domestication also resulted in changes in reproduction and the level of pungency [76,77,83,84].

Currently, *Capsicum* includes about 25 wild species and 5 species with domesticated populations: *Capsicum annuum, C. frutescens, C. chinense, C. baccatum* and *C. pubescens*. The *C. annuum-chinense-frutescens* complex may have arisen from a widely distributed complex of closely related wild and weedy species [85]. In an attempt to resolve this question, the chloroplast *atpB-rbcL* noncoding spacer region was used to examine the phylogeny of *Capsicum*, using 11 *Capsicum* species and seven outgroups [86]. The *annuum* group consists of *C. annuum, C. chinense, C. frutescens*, and *C. galapagoense*, without clear morphological unity but with strong support from isozymes. Only the wild progenitor of *C. annuum* is known: *C. annuum* var. *aviculare*. Without identification of the wild progenitor, identification of the center of origin of a domesticated population is extremely difficult [80].

The center of diversity of *Capsicum* is in South America, with most species in Brazil and Bolivia. Studies in cytogenetics, molecular genetics, archaeology and biogeography established probable centers of origin of each domesticated species [80]. The center of origin of the economically most important *C. annuum* (chili, jalapeño, cayenne) is in Mesoamerica, more precisely in upland central-eastern Mexico [87], confirmed by molecular analysis. The centers of origin of the other domesticated lowland species are not yet clear, but it is believed that Amazonia is the center for *C. chinense* (cumari, murupi, habanero, biquinho), where its variability is greatest, and Amazonia may be

the center for *C. frutescens* (cayenne, tabasco) [78], although Mesoamerica is also a candidate given abundant morphological diversity [10]. Remains of a reputed *C. chinense* were found at Guitarrero Cave, in the western Andean foothills of northern Peru and dated as earlier than 9000 BP, while *C. frutescens* only appears in the same region (Huaca Prieta) at about 3,500 BP [6]. Recently, an apparently wild sample of *C. chinense* was found in Roraima, Brazil [88], offering the possibility of a more precise origin for this species, but a wild population of *C. frutescens* has not yet been found in Amazonia or Mesoamerica. Subsequently, both species were distributed from the Amazonian lowlands to southeastern Brazil, Central America and the West Indies [76,89], but the famous habanero arrived in Mexico only after the conquest, which explains its name, as Habana is the current capital of Cuba, where the Taíno people, of the Arawakan language family, had introduced it before European conquest. Southwestern Amazonia, more precisely the lower Andean valleys of Bolivia, is considered the center of origin for *C. baccatum* (girl's finger, chili or ají) and its distribution was less extensive before European conquest [9,82,89]. The earliest archaeological remains of *C. baccatum* are from Huaca Prieta and Punta Grande, in the western Andean foothills of Peru, dated to before 4,000 BP [6].

2.5. Pineapple

At the time of European conquest, the pineapple (*Ananas comosus* var. *comosus* (L.) Merr., Bromeliaceae) was cultivated in all the Neotropical lowlands, from Mesoamerica and the Antilles southward to Paraguay and the humid valleys along the Pacific coast of Peru, and specific cultivars had been developed for the Andean hillsides, where they are still important in Colombia, Venezuela and Peru. Its Latin name is derived from the word *nana* and its derivatives, such as *nanas*, *ananas*, or *nanaí*, which are widely distributed in most languages of South America and the Antilles. Europeans first learned of this fruit when Columbus arrived on the island of Guadeloupe in 1493. By the end of the 16th century the pineapple was pantropical and its development as a first-rank world fruit crop has been based on pre-Conquest Native American cultivars [90,91].

Wild forms of *A. comosus* are found in all the Neotropical lowlands east of the Andes, from the northern shores of South America to southern Brazil and Paraguay, with the exception of the floodplains of the Amazon and Solimões Rivers and their southern tributaries, where seasonal floods limit natural dispersal [90,92]. More morphological, physiological and genetic variation is observed north of the Amazon River, with two wild botanical varieties, *A. comosus* var. *parguazensis* and *A. comosus* var. *ananassoides*, while only the latter occurs south of the Amazon. *A. comosus* var. *parguazensis* is distributed in the basins of the Orinoco River (the variety name derives from the Parguaza tributary) and the upper Negro River. Similar morphotypes occur in the Guianas, but they developed from a different genetic background [93]. Compared to var. *ananassoides*, var. *parguazensis* is restricted to more humid and shadier habitats, due to its lower water use efficiency [94]. *A. comosus* var. *ananassoides* prefers xerophytic edaphoclimatic conditions, thriving on sand dunes and campinas, rocks and inselbergs, although it may also be found in denser forest. North of the Amazon, it displays much greater morphological and genetic variation than in the south. In particular, many northern clones exhibit appreciable growth of the syncarp after anthesis, resulting in larger and fleshier fruit, while south of the Amazon the fruits are always small and very fibrous, and

the plants show ecological specialization, being restricted to open dry habitats, from arid savannahs to cerrados [94,95].

The distribution of morphological diversity within *A. comosus* suggests that the species originated in the north [96]. The south is the region of origin of another species, the *yvira* or *nana caçaba* (*A. macrodontes* Morren), not found in the north. This tetraploid lacks a fruit crown and reproduces vegetatively by stolons, forming relatively large stands. Its habitat is the understorey of the humid Atlantic Forest of coastal Brazil and the Parana-Paraguay drainage in southern Brazil, Paraguay and northern Argentina. It was exploited for fiber by the natives [97], but shows no sign of domestication.

Based on a revision of morphological [95], biochemical [98] and genetic diversity [99], Coppens d'Eeckenbrugge *et al*. [90] and Coppens d'Eeckenbrugge and Leal [100] proposed that the north, and more specifically the Guiana shield, is also where the pineapple was domesticated. Coppens d'Eeckenbrugge and Duval [92] refined this hypothesis to take into account recent data on chloroplast DNA variation [93]. The eastern part of the Guiana shield contains considerable phenotypic and genetic diversity, including wild phenotypes with relatively large and fleshy fruits that would have attracted foragers, primitive cultivars and a wide range of large-fruited cultivars. The practice of picking clones in the wild and transferring them to home gardens is still common in eastern Guiana, and many primitive cultivars can survive under secondary forest canopy. This long-term exchange between wild and cultivated populations is confirmed by genetic studies: all four chloroplast haplotypes identified in cultivated materials are present in the wild var. *ananassoides*, supporting the hypothesis that the domesticated var. *comosus* was derived from var. *ananassoides* through selection among those clones with markedly larger syncarps [93].

The domestication syndrome shows both human selection and correlated responses. Greater fruit size resulted from selection for larger individual fruits (pineapple "eyes") and an increase in their number, which also changed their phyllotaxy. A larger number of wider, and generally shorter, leaves provide energy, and a stouter and longer stem allows greater starch storage capacity during the vegetative phase. The latter has been extended by reduced susceptibility to natural flowering induction. Seed production has been reduced through the combination of lower sexual fertility and stronger self-incompatibility [101].

Coppens d'Eeckenbrugge and Duval [92] proposed that var. *comosus* diversified dramatically in western Amazonia, especially in the northwestern center of crop diversity [1] and along the lower Negro River; in both areas a great diversity of advanced cultivars was developed in the absence of wild forms [95]. The peoples of western Amazonia demonstrated brilliant horticultural and plant-breeding skills, as this region is also an important center of domestication and diversification for many other fruits [1,5]. There, pineapple is still a major fruit crop for peoples like the Tikunas [95] and the Huitotos [102], who maintain a wide diversity of cultivars, and it ranks among the primary culturally defined keystone species for peoples like the Letuama. This type of keystone species is one whose existence and symbolic value are essential to the stability of a cultural group over time [103].

The widespread distribution of the pineapple in the Americas at the time of the European conquest, the diversity and quality of the cultivars, not surpassed after one century of modern, intensive breeding, the diversity of uses, the economic and cultural importance of the crop, all point to a very ancient domestication. However, archaeological findings are rather late: 3,200 to 2,800 BP in the valleys of the arid Peruvian Coast [6]; and 2,200 to 1,300 BP from the Tehuacán Valley caves

(Mexico) [104]. The glottochronology of pineapple in Ancient Mesoamerica suggests that the crop was significant by 2,500 BP [42]. Thus, domesticated pineapple was traded and adopted as an important fruit crop on a continental scale more than 3,000 BP. Given the rarity of sexual reproduction in *A. comosus* var. *comosus*, the development of tradable cultivars was necessarily a long and slow process, certainly counted in millennia. Thus, a likely time frame for the divergence between wild and cultivated pineapple lies between 6,000 and 10,000 BP.

Other domestication processes must be considered in *A. comosus*, as there are two other cultivated botanical varieties in the species. The most important is the *curagua* (*A. comosus* var. *erectifolius* [L.B. Smith] Coppens and Leal) developed as a fiber crop via selection from *A. comosus* var. *ananassoides*. It was commonly cultivated north of the Amazon and Solimões rivers, as well as in the Antilles in pre-Columbian times. Its characteristic dense, erect and smooth foliage are the likely result of selection for an abundance of long easily-extractable fibers. Genetic affinity of the curagua with different lineages of var. *ananassoides* indicates multiple and independent domestication events [93,99]. Their antiquity is probably variable, as some clones have reduced fruit production, while others are remarkably fertile.

The domestication process for *A. comosus* var. *bracteatus*, also cultivated for its fiber in Paraguay [97], may have simply consisted of the direct vegetative propagation of rare interspecific hybrids, as this botanical variety has very limited variability. It is native to southern South America and shares nuclear markers with the yvira, indicating ancestral interspecific introgression with this species. Furthermore, the chloroplast haplotype of the rarest form is very similar to that of *A. macrodontes* [93].

The genus *Ananas* is ideal for domestication studies, with multiple processes in time and space, and specialization related to the major uses as a food or as a source of fibers. Selection for fruit characteristics took place where the diversity and quality of spontaneous materials allowed it. The fruit quality induced the crop's dispersal, which in turn induced further diversification and environmental specialization. The development of extremely derived cultivars, in terms of both fruit size and quality, and more particularly the secondary diversification in western Amazonia, despite the lower fertility of advanced cultivars, inevitably raises the question of the capacity of native breeders to exploit sexual recombination, because germination is not easy and seedlings are fragile and grow slowly. The pattern is different for the production of fiber. The domestication process, involving fewer morphological changes, was probably more straightforward for curagua, and could be repeated more easily in time and space, on different lineages of the wild forms. The curagua was widely dispersed, although not so widely as the fruit cultivars, possibly because curagua is not transported/exchanged unintentionally with its propagules, while fruits travel with their crown, and because of competition among domesticated lineages, especially south of the Amazon where large wild stands of *A. macrodontes* or subspontaneous stands of *A. comosus* var. *bracteatus* offered more economical sources.

2.6. Inga

The genus *Inga* includes around 300 species throughout the Neotropics [105] and a history of use by American peoples for at least eight thousand years, mainly for their edible fruits [106]. In Amazonia, *Inga edulis* Mart. (hereafter simply inga) is certainly most important. This is a diploid

legume, predominantly outcrossing and pollinated by small birds, flying insects and bats [107]. It is cultivated for its fruits and wood in indigenous and traditional communities throughout Amazonia, and is considered a priority in many communities of Peruvian Amazonia [108-110]. The history of cultivation of this species is not registered, but morphological studies show that humans have selected inga for a considerable period of time, creating several semi-domesticated populations [1,5,105]. Trees planted in the Peruvian Amazon bear some of the largest pods observed anywhere, and pods under cultivation are much longer and thicker than those in wild populations [105]. Due to these traits, inga has become a model species to evaluate the efficiency of agroforestry systems for the maintenance of genetic resources, as well as for identifying possible origins and bottlenecks associated with domestication.

Hollingsworth *et al*. [111] used five SSR loci to evaluate the maintenance of the genetic diversity in five planted and five natural populations in the Peruvian Amazon. They found less variation in the planted populations compared with the natural [mean corrected allelic richness of 31.3 (planted) and 39.3 (natural), p = 0,009], exactly what is expected in domesticated plant populations [112]. Although lower levels of allelic variation occur in planted populations than in the natural populations, the former still contain on average 80% of the existing allelic diversity found in wild populations. The mean values of expected heterozygosity (0.65 planted *versus* 0.67 natural) indicate that they have not experienced extreme bottlenecks, possibly due to high tree density and the size of the planted populations, and the contribution of pollen and seeds of adjacent plantations and neighboring wild populations.

Nuclear SSRs and chloroplast DNA were used to evaluate the origin of five pairs of planted and wild populations in the Peruvian Amazon, with the intention of determining whether these were derived from local wild populations [113]. The cultivated populations did not have local origin. Nuclear and chloroplast diversity were lower in the planted populations, ~80% and ~70% of the natural populations, respectively, similar to the earlier study [111].

The genetic analyses confirm that inga has domesticated populations, although they do not confirm its degree of domestication, which was suggested to be semi-domesticated [1]. A broad phylogeographic study is needed to understand inga domestication better and to identify the probable origin of the domesticated populations.

2.7. Guaraná

Guaraná (*Paullinia cupana* Kunth var. *sorbilis* [Mart.] Ducke, Sapindaceae) was domesticated in the region between the lower Tapajós and lower Madeira Rivers in Central Brazilian Amazonia by the Sateré-Mawé, a people of the Tupi language stock [114]. The first European to mention guaraná was the Jesuit João Felipe Bettendorff [115] in 1669, who observed that the Sateré-Mawé were the original cultivators of the vine; he did not mention any other ethnic groups cultivating guaraná. The Mundurucu, another Tupi language group, occupy the area immediately south of the Sateré-Mawé and do not cultivate guaraná traditionally [116]. Guaraná is important in Sateré-Mawé mythology because of its relation with their origin.

As recounted by the Sateré-Mawé to the Brazilian ethnographer Nunes Pereira [117] in 1939, the genesis of guaraná involves rivalries between two brothers and their sister, Onhiamuaçabê. The

brothers did not want anyone to marry their sister because she knew all the plants, and which of them were good for curing. She was also the owner of an enchanted place called Noçoquem, where she had planted a Brazil nut tree. One day, a small snake took a fancy to her, so he released a perfume along a trail used by Onhiamuaçabê. She liked the scent a lot. So the snake went further up the trail and touched her lightly on the leg as she passed by. She was immobilized so the snake took advantage of her and she was impregnated. The brothers were furious.

Onhiamuaçabê gave birth to a beautiful boy, and when the boy was old enough, she took him to the enchanted place to eat Brazil nuts. An agouti noticed someone had made a fire at the base of the Brazil nut tree to roast nuts and he reported what he had seen to the brothers. They had guards posted at the enchanted place, and when the boy came the next day to eat some more nuts they decapitated him. His mother heard his cries of anguish, but it was too late. By the time she reached the enchanted place, he was dead. She plucked out the boy's left eye and planted it. But the plant that germinated was no good; it was false guaraná. She then plucked out the right eye and planted it; this grew into true guaraná. She spoke out aloud, as if the child was still alive: "You, my son, will be the greatest force of Nature; you will do good for all men; you will be great; you will free men from some sicknesses and cure them of others". And out of the buried corpse of the boy arose the first Sateré-Mawé.

The meaning of this myth recently became remarkably clearer. The *sorbilis* variety of guaraná grown by the Sateré-Mawé is a high level polyploid, with 210 chromosomes rather than the standard 24 for the genus; the numbers and morphology of the chromosomes suggest the combination of a tetraploid and an hexaploid [118], that may be from different genera [114]. In essence, this myth captures the guaraná domestication event, which occurred when the mythological woman recognized that a special type of guaraná had become available to her, as distinct from the more common and less useful false guaraná, and that it should be planted for the benefit of future generations. True guaraná is remarkably different from the false guaranás (other *Paullinia* spp) that grow wild in the Sateré-Mawé territory, so much so that any observer can readily distinguish the two morphologically by the larger fruit and seeds, and the brightly colored fruit case of true guaraná. Sexually reproducing polyploids commonly show remarkable morphological variability [3,119], which has been observed in guaraná [114,120], and may have different ecological adaptations [119], which have also been observed in guaraná, since it is well adapted to indigenous agroecosystems and does not survive long in second growth forests.

When might the domestication event have occurred? Food production systems became more important than foraging after about 4,000 years ago [121]. This time frame corresponds to the expansion of the Tupi language trunk [122], which started from what is now Rondônia in southwestern Amazonia. The Sateré-Mawé may have arrived in their current location about 2,000 years ago, which provides a reasonable maximum age for the domestication event mentioned in the myth, although a Sateré-Mawé elder thinks that it may have been only 600 years ago [123]. Considering that other Tupi groups in the vicinity do not consider guaraná to be as important as it is to the Sateré-Mawé, it seems probable that the domestication event occurred after the arrival of the Sateré-Mawé in the present location. Supporting evidence for a possibly later domestication is the lack of molecular genetic variability observed in the *sorbilis* variety among samples collected in three areas of Central Amazonia, including Mawés [120], the municipality in which the Sataré-Mawé live. In this study, Sousa used 16 RAPD primers to generate 150 markers (mean 9.4 markers per primer; minimum five;

maximum 13), which is reasonable for a diploid (for example, Rodrigues *et al*. [59] generated 14.1 markers per primer in peach palm). For a high level polyploid to exhibit a diploid range of bands, there must not have been mutation in the primer sequences since the polyploid event, again suggesting that it is recent. The study examined 75 clones obtained from Maués (47), Iranduba (6) and Manaus (22), and used the Dice similarity coefficient to examine the genetic relationships among these clones. The Dice similarity dendrogram showed most clones to be closely related (90% of the possible combinations had similarities greater than 0.6) and there was no geographic structuring. The lack of geographic structure suggests a recent dispersal from Maués, which is in agreement with colonial period reports that initially only the Sateré-Maué cultivated guaraná [116] and again suggests a very recent origin.

2.8. Brazil Nut

The Brazil nut (*Bertholletia excelsa* Bonpl., Lecythidaceae) is Amazonia's most important extractive product, contributing to the livelihood and food security of thousands of families in the interior of the region [124]. Brazil nut occurs as both scattered trees in upland forests and as anthropogenic stands, called *castanhais* [8,125]. Müller *et al*. [126] hypothesized that Brazil nut's current distribution is largely due to human dispersal, which is strongly supported by the distribution of *castanhais* and the lack of old growth Brazil nut in some areas, such as part of the municipality of Manaus [127] and much of the Juruá River basin [128]. Along the Purus River, in southern Amazonia, several populations have quite large seeds, suggesting incipient domestication [1].

Brazil nut's most important modern non-human seed dispersal agents are thought to be agoutis [125], small forest rodents, which are the only animals known to open the Brazil nut fruit. The choice of dispersal agents allows the elaboration of two hypotheses about Brazil nut's population structure in Amazonia, as each agent has clearly different dispersal abilities. (1) If agoutis were and are the most important dispersal agents, Brazil nut should show a fine-grained population structure, with numerous sub-populations along the interfluvials as well as through the headwaters. (2) If humans were (and are) the primary dispersal agents, Brazil nut should show a relative lack of population structure, because humans have only acted within the last 10,000 years or so, which is recent in terms of Brazil nut generations.

Ongoing work by the group led by Maristerra Lemes and Rogério Gribel, at the Instituto Nacional de Pesquisas da Amazônia, has found compelling molecular genetic evidence in support of humans as the primary dispersal agents of Brazil nut in Amazonia [129,130]. Preliminary analysis of eight widely separated populations (maximum separation 2800 km) with various chloroplast markers showed a startling lack of genetic structure. Based on chloroplast SSRs, 94% of genetic variation was found within populations, while only 6% was found among populations, which contrasts with among population variation of 10–15% in tropical tree species not propagated by humans and examined at similarly large scales (references in [131]). Several chloroplast sequences were invariable across the entire data set.

Two previous studies provide somewhat similar evidence. Buckley *et al*. [132] used several isoenzymes to examine genetic variation within and between two populations. They found only 3.75% of the genetic variation between the populations, which were less widely dispersed than the populations used by Lemes and Gribel's group. Kanashiro *et al*. [133] used 47 RAPD markers to

assess variation in five widely distributed populations, and used Shannon's H diversity index to estimate RAPD phenotypic diversity and to partition this within and among the populations. They found 31.3% of the variation among populations, considerably higher than the other studies. It is not clear why this among population measure is so different, but it may be due to the RAPD markers (which are less informative) and the Shannon index.

The sum of these studies suggests that humans distributed Brazil nut widely during the Holocene, strongly supporting Müller *et al*.'s [126] hypothesis. The anomalies in Brazil nut's modern distribution also support this hypothesis, since only human preferences can explain the absence of the species in some areas. None of these studies, however, provide any information on Brazil nut's origin. Scott Mori [134] hypothesized that Brazil nut may have originated in southeastern Amazonia. Only much more intensive population sampling and genetic analysis will permit the confirmation of this hypothesis or the elaboration of a new one.

2.9. Cupuassu

The cupuassu [*Theobroma grandiflorum* (Willd. ex. Spreng.) Schum., Malvaceae] is currently one of the most important native fruits in Amazonia, with about 35,000 ha of orchards planted over the last three decades [135]. Fruits in homegardens and orchards tend to be much larger than those collected from the forest in its reputed center of origin in southern and southeastern Pará [136], which led Clement [1] to suggest that numerous populations were incipiently domesticated before European conquest. A recent molecular genetic analysis [137] suggests that this may not be the case.

In the mid-1700s, Padre João Daniel [138] affirmed that cupuassu was not cultivated by native peoples or colonists, and suggested that its cultivation would be worthwhile. In the pre-Amazonian part of Maranhão, however, Balée [139] observed cultivation of cupuassu in Ka'apor homegardens, within the reputed center of origin of the species, although it is not known if cupuassu is a traditional crop among the Ka'apor. In the mid-1900s, Adolfo Ducke [140] (1946) commented that cupuassu was rare in western Amazonia, although it was then being dispersed along the main rivers. In fact, most cupuassu in the markets of Pará was derived from extractivism until the 1970s [135]. These somewhat conflicting observations suggest the need to reevaluate cupuassu's incipient domestication. Molecular evidence will help with this task, although only one study has been conducted to date [137].

Alves *et al*. [137] used 21 SSR loci to examine three natural populations from cupuassu's reputed center of origin in Pará (Novo Ipixuna, Tucuruí, both Pará, and pre-Amazonian Maranhão), as well as three germplasm collections created separately over the last 30 years and maintained at different Embrapa stations (Amapá, Pará, Amazonas), and one extensive sample from farmers' orchards within the center of origin (Tomé-Açu, Pará). The genetic parameters estimated for these materials contained surprising patterns, with considerably less within-population diversity (70%) than expected (80–90% is common in tropical trees [131]) and considerably more among-population diversity (30%), and high levels of inbreeding (f = 0.192) within the three natural populations. Genetic distances among the natural populations and the farmers' orchards in the center of origin were considerable (Nei's [66] unbiased genetic distances varied from 0.198 to 0.234). This high among-population divergence may be partially due to cupuassu's pollinators (small bees and flies) and modern seed dispersal agents (small rodents), which minimize gene flow among populations, allowing genetic drift to enhance

divergence among inbred populations. The magnitudes of these genetic parameters may be a recent phenomenon, however, as cupuassu may have been dispersed by now-extinct Pleistocene megafauna [141], whose larger size may have permitted greater dispersal distances.

In contrast to these natural populations, the three germplasm collections were significantly more homogeneous (Nei's [66] distances of 0.012 to 0.033 among them), suggesting little genetic divergence over enormous distances (Amapá to western Amazonas along the Amazon and Solimões Rivers). The three collections are based upon different collection expeditions, with the Amapá and Amazonas collections containing principally state-sourced germplasm, while the Pará collection contains both state-sourced germplasm and samples from the Solimões River; there is little replication among the collections. The germplasm collections also had more alleles per population, fewer private alleles, and similar observed heterozygosities. This set of information suggests considerable gene flow over large distances, now mediated by human dispersal. Curiously, neither the Pará nor the Amapá germplasm collections had close genetic relationships with the natural populations (Nei's [66] distances of 0.350 to 0.376), suggesting that a different set of natural populations were the source of the cupuassu distributed along the main rivers during the colonial and modern periods.

This molecular analysis and the conflicting information about cupuassu's history call into question cupuassu's classification as a species with incipiently domesticated populations [1], but are not sufficient to reclassify it as wild. As cupuassu's importance increases in modern Brazilian Amazonia, new germplasm collections are planned that will hopefully permit future analyses to determine cupuassu's status as a native domesticate.

3. Patterns of Diversity

Although the number of species with molecular genetic analyses is still small, some patterns are congruent with previous thinking about the origin, domestication and dispersal of native Amazonian crops. The first important pattern is the antiquity of several important Amazonian domesticates, such as manioc (more than 8,000 BP), *Capsicum* (more than 6,000 BP), pineapple (possibly more than 6,000 BP) and, perhaps, peach palm (possibly as early as 10,000 BP). The first two have archaeological support from coastal Peru, while the latter two are projections based on morphological differences among wild and fully domesticated populations. No estimates of the dates of the primary domestication event with genetic coalescence analysis have been presented to date, but this type of analysis will certainly be attempted within the next decade.

Although these dates are quite old, they are more recent than the initial peopling of Amazonia, which occurred before 11,200 BP when the Pedra Pintada site was occupied in Central Amazonia, in what is now Monte Alegre, Pará [142]. These early occupants were broad-spectrum foragers, who may have begun domestication of the landscape near the site [143], but who did not possess any plant populations with signs of domestication. Somewhat later (7,100 BP) and on the other side of the Amazon River at Taperinha, near Santarém, Pará, settled villages appeared, based on exploitation of fluvial resources and forest foraging, as well as the first pottery in the Americas [144]. Some of the pottery suggests the presence of food production, but no evidence of domesticated plants exists [143]. Again, we can assume that landscape domestication was certainly underway. The lack of domesticated

crops in settings where dump heaps were certainly becoming home gardens [145] is curious, as at least manioc was already being dispersed from its origin in southwestern Amazonia.

This leads to a second important pattern: the relation between antiquity and origin. All but one of the species examined originated in the periphery of Amazonia (Figure 3), rather than along the major white water rivers where pre-conquest population densities were greatest. The exception is guaraná, a very recently domesticated crop, although cupuassu may be a similar case. The most important crops with domesticated populations are also the oldest, and all come from the periphery: manioc, pineapple, *Capsicum*, peach palm, tobacco, perhaps sweet potato. The importance of the periphery has been highlighted previously [121], with emphasis on extreme northwestern Amazonia and the adjacent Llanos of the Orinoco River basin, the Guiana shield and southwestern Amazonia, especially the Llanos de Mojos, in Bolivia. Work on Amazonian fruits permits the addition of numerous species with domesticated populations to the list, as well as several semi- and incipiently domesticated populations [1,146], without changing the emphasis on the periphery, although this region has now been expanded to include the Andean foothills and immediately adjacent lowlands in western Amazonia and some of southeastern Amazonia (Figure 3).

Figure 3. Confirmed and hypothetical origins of some native Amazonian crops. The confirmed origins are (from north to south): pineapple, cubiu (*Solanum sessiliflorum*), cacao, assai (*Euterpe oleracea*), guaraná, manioc, coca (*Erythroxylum coca*), tobacco (*Nicotiana tabacum*), peanut (*Arachis hypogaea*). The hypothetical origins are: genipap (*Genipa americana*), leren (*Calathea allouia*), sweet potato (*Ipomoea batatas*), cocoyam (*Xanthosoma sagittifolium*), yam (*Dioscorea trifida*), murupi pepper (*Capsicum chinense*), mapati (*Pourouma cecropiifolia*), abiu (*Pouteria caimito*), bacuri (*Platonia insignis*), inga (*Inga edulis*), cashew (*Anacardium occidentale*), sapota (*Quararibea cordata*), cupuassu, biriba (*Rollinia mucosa*), guava (*Psidium guajava*), Brazil nut, peach palm, cocoyam, annato (*Bixa orellana*), malagueta pepper (*Capsicum frutescens*). Note that there is continued uncertainty about Mesoamerican origins for guava and malagueta pepper.

Whether the peripheral origin of the earliest domesticated populations is due to the plants themselves or to human activity is an interesting question. During the terminal Pleistocene, when humans were already in Amazonia, much of western Amazonia is thought to have been forested, while

large parts of central and eastern Amazonia were open forest that was quite different from current open forests [147-149]. The drier areas along the northern and southern peripheries probably expanded further into the basin than they do currently. The crops that were domesticated early, e.g., manioc, peach palm, pineapple, probably *Capsicum*, originated in these open ecosystems, some of which remain in place, others of which have been transformed into more humid forest as this expanded during the Holocene. Some of the difficulties in identifying origins may be due to forest expansion during the Holocene, although better geographic sampling may resolve many of these difficulties.

Root and tuber crops generally originated in seasonally dry open ecosystems, where they fill their starchy storage organs before the dry season, making them attractive to hunter-gatherers during the dry season [121]. This also makes them well adapted to human modified niches in the landscape, such as dump heaps that later became home gardens [145] and incipient horticultural systems. Manioc was also selected for growth in anthropogenic soils (terra preta de índio), some of which also originated as dump heaps [150], and floodplain soils [33], although most landraces are well adapted to nutrient poor upland soils. It is probable that the other root and tuber crops also had some varieties adapted to floodplain soils, but they may have been lost in the post-conquest wave of genetic erosion that accompanied population decline [1].

The humid periphery in western Amazonia appears to be home to numerous fruit crops and different adaptations might be expected. Some, like cacao, survive well in humid forest under-stories, whereas others, like inga, have adapted well to open horticultural systems. Many of those that have not yet been subjects of genetic analysis appear to have originally adapted to successional ecotones, as they do not survive long when the second growth forest grows enough to shade them out. The exception is sapota, which is a canopy emergent when mature.

As highlighted above, however, early occupation of central Amazonia did not include domesticates, even though the ecosystems around Pedra Pintada and Taperinha were probably relatively more open at the time than currently, and landscapes within them were probably being domesticated. It is possible that sufficient natural resources were available so that the home gardens were such a small fraction of subsistence that they are difficult to find in the archaeological record. In contrast, in the headwaters of the same rivers in the periphery, less abundant aquatic resources may have increased the importance of home gardens. In fact, the earliest terra preta de índio is also in the periphery, along the Jamari River, in the upper Madeira River basin [151]. Rindos [51] and Tudge [152] hypothesize that foragers who also practiced plant domestication would be more successful than those who did not, and it was from the southwestern periphery that two language diasporas occurred: Tupi-Guaraní and Arawak-Maipuran [122]. The southern and southwestern periphery eventually was the stage for the development of complex societies as well [153], but a detailed search is still required for signs of *in situ* crop domestication, with *Caryocar brasiliense* mentioned as a possible candidate.

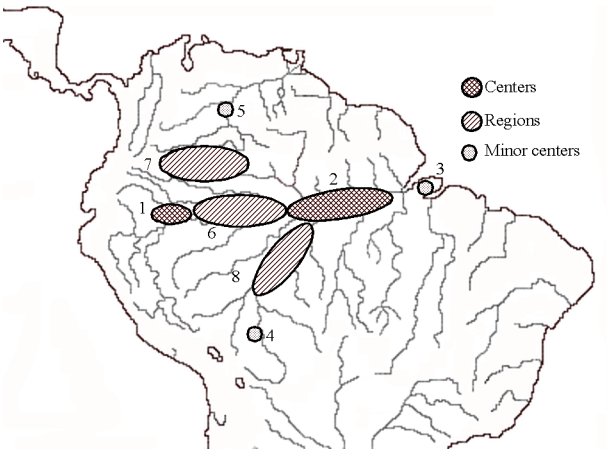
A pattern whose explanation is less clear is why certain crops were widely dispersed and others not. Crops with good adaptation to environmental variation, e.g., manioc, were widely dispersed quite rapidly, appearing in the archaeological record of the Pacific coast of Peru by 8,000 BP or earlier [6] and southern Mesoamerica by 5,600 BP at the latest [154]. Those with early adaptation to human disturbance, e.g., *Capsicum*, were certainly excellent camp followers, although it is difficult to determine which peppers appear first on the coast of Peru, since only the genus is mentioned for the earliest records [6].

It is probable that ethnic preferences determined dispersal patterns. For example, peach palm's double dispersal of smaller oilier fruits down the Madeira River and along the Amazon River, and larger starchier fruits down the Ucayali River, throughout western Amazonia, along the Pacific coast of Ecuador and Colombia, and into Central America, but not the Caribbean islands, may be related to the Tupi and Arawak dispersals, respectively [53], even though these dispersals are much later than the initial domestication events. The absence of Brazil nut in the Juruá River basin is another example.

Genetic evidence also sheds light on dispersal patterns. When a domesticate was important and taken into cultivation early, generally clear genetic structuring occurs among populations, such as the landraces of peach palm. When the crop was important, early and also annual, numerous varieties were developed and spread locally, but less regional structuring is evident, as seen in manioc, although superimposed on the bitter-sweet distinction, and in *Capsicum* and pineapple. When the crop is an incipient domesticate or became important only recently, no clear genetic structuring occurs, as in Brazil nut, cupuassu and guaraná.

What is quite clear, however, is that the major pre-conquest population centers concentrated crop genetic resources to guarantee their subsistence and trade (Figure 4). The major centers and regions of diversity are along the major white water rivers and in northwestern Amazonia, where ethnic diversity is extremely high [7]. The minor centers are all related to areas where pre-conquest populations transformed the landscape with earthworks of various types [7]. It may also be appropriate to consider the upper Xingu River a minor center, given the intensity of landscape domestication, complex social structure, and possible incipient domestication of local fruit trees, such as *Caryocar brasiliense* [155]. The fact that the majority of Amazonia is not included in these concentrations does not imply that crop genetic resources were absent, but that they had not been concentrated to the same degree, principally because human population densities were lower.

Figure 4. Centers, regions and minor centers of crop genetic resources diversity at the time of European conquest (modified from [7]). Centers of diversity: 1—western Amazonia; 2—central Amazonia. Minor centers: 3—Marajo Island; 4—Llanos de Mojos; 5—middle Orinoco River. Regions of diversity: 6—Solimões River; 7—upper Negro River; 8—Madeira River.



The contrast between the presumed origins of native Amazonian crops in the periphery (Figure 3) and their concentration in the centers of pre-conquest population density (Figure 4) is dramatic.

Clearly, centers of origin and centers of diversity are not equivalent concepts, as Nikolai I. Vavilov [156] understood, although many students of crop genetic resources throughout the 20th century claimed otherwise. Because crop domestication began thousands of years before food production systems became important [51,121], it is not at all surprising to see a dramatic contrast such as that in Amazonia. As the archaeology of Amazonia becomes better understood [153] and as the number of species studied with genetic and phylogeographic methods expands, we will certainly be able to clarify the patterns mentioned here and perhaps identify others.

4. Conclusions

The available information concerning the origin and domestication of manioc (*Manihot esculenta*), pineapple (*Ananas comosus*), peach palm (*Bactris gasipaes*) and guaraná (*Paullinia cupana*) is reasonably solid, while that of cacao (*Theobroma cacao*) requires rethinking presuppositions about what domestication means in that crop. The information available for hot peppers (*Capsicum* spp.), inga (*Inga edulis*), Brazil nut (*Bertholletia excelsa*) and cupuassu (*Theobroma grandiflorum*) is growing and provides substantial clues as to their origins and domestication. Emergent patterns include the relationship among domestication, antiquity, origin in the periphery, ample pre-Columbian dispersal and clear phylogeographic population structure, which often corresponds to phenotypic entities recognized by cultivators, *i.e.*, landraces (or groups of landraces), e.g., manioc, pineapple, peach palm and, perhaps, *Capsicum* peppers. Another pattern is the relationship among crops with incipiently domesticated populations, or very recently domesticated populations, rapid pre- or post-Columbian dispersal and lack of phylogeographic population structure, e.g., Brazil nut, cupuassu and guaraná. Cacao represents the special case of an Amazonian species possibly brought into domestication in Mesoamerica, but close scrutiny of molecular data suggests that there may also be incipiently domesticated populations in Amazonia. Additional molecular genetic analyses on these and other species will allow better examination of these processes and will enable us to relate them to other historical ecological patterns in Amazonia.

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Isozyme variation in *Passiflora* subgenera *Tacsonia* and *Manicata*. Relationships between cultivated and wild species

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Abstract

Isozyme variation was studied in 87 plants from 32 cultivated and wild accessions of banana passion fruit (*P. tripartita* var. *mollissima*, *P. tripartita* var. *tripartita*, *P. tarminiana*, and *P. mixta*), rosy passion fruit (*P. cumbalensis*), tin-tin (*P. pinnatistipula*), gulián (*P. ampullacea*), *P. antioquensis*, *P. bracteosa*, and *P. manicata*, from the Andes of Venezuela, Colombia, and Ecuador. Six polymorphic enzyme systems (IDH, PGDH, PGM, DIA, PRX, and ACP) revealed 31 zymotypes characterized by the presence or absence of 31 electromorphs. Cluster analysis separated clearly the accessions of *P. tarminiana*, *P. tripartita*, *P. mixta*, and *P. cumbalensis* from the less typical species of subgenus *Tacsonia*, which is consistent with morphological evidence. *P. mixta* showed the highest intraspecific variation and the closest affinity with *P. tripartita*. The accessions of these two species formed two clusters, one dominated by Colombian genotypes and the other dominated by Ecuadorian genotypes. One of the *P. tripartita* var. *mollissima* accessions clustered close to *P. tarminiana* accessions. The affinity between these three species is particularly interesting for conservation and use of banana passion fruit genetic resources. All the other species formed monospecific clusters.

Introduction

Martin and Nakasone (1970) estimated that 50 to 60 species of *Passiflora* (out of more than 400) produce an edible fruit. Other species are of great ornamental interest (Vanderplank 1996). Due to its outstanding horticultural potential, the national plant genetic resources programs of the Andean countries have prioritized this genus in their exploration and use of biodiversity for development.

Killip (1938) recognized 22 subgenera within *Passiflora*. Most fruit species belong to the subgenera *Passiflora* and *Tacsonia*. The former is well known for such species of economic importance as the yellow and purple maracujas (*P. edulis* Sims), the sweet granadilla (*P. ligularis* Juss.), the giant granadilla (*P. quadrangularis* L.) and the fragrant granadilla (*P. alata* Dryand.), while the latter is mostly known for the banana passion fruit. This consists of two species, *P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen and the recently described *P. tarminiana* Coppens & Barney, respectively named 'curuba de Castilla' and 'curuba india' in Colombia, and 'tacso de Castilla' and 'tacso amarillo' in Ecuador (Coppens d'Eeckenbrugge et al. 2001).

The natural distribution of the subgenus *Tacsonia* is restricted to the Andes of South America, with about 50 species growing above 2000 m of altitude (Escobar 1992). The most conspicuous morphological difference between the subgenus *Tacsonia* and most other subgenera lies in the relative length of the hypanthium and the reduction of the corona. Characteristically, the hypanthium is longer than the sepals, the corona is generally reduced to a single row of small tubercules, and no significant stigmatic movement is observed during anthesis, as is the case in

Table 1. Taxonomy, ecology, distribution, and main elements of morphological variation for the taxa under study, following Escobar (1988), Holm-Nielsen et al. (1988). A more complete description is given for *P. tripartita* var. *mollissima*. Only the morphological divergences from this typical species and exceptional traits are given for the other taxa.

Species/section	Distribution/ecology	Main morphological traits
P. tripartita – var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen (curuba de Castilla)	Commercial cultivation (Venezuela to Ecuador), homegardens (Peru, Bolivia), 2400–3500 m.	Pubescent, leaves trilobular, stipules reniform, aristate, bracts united, flower pendent, floral tube long, corolla much shorter, pink, corona reduced to a single row of tubercules, fruit oval, elongated, pale yellow, aril succulent.
– var. *azuayensis* Holm-Nielsen & Jørgensen – var. *tripartita* Section *Bracteogama*	Wild / homegardens (central and southern Ecuador) Montane forest, 2400–3500 m.	Partially pubescent, leaf lobes narrower, fruit smaller, yellow to orange, aril less succulent.
P. cumbalensis (Karst.) Harms (curuba roja) Section *Bracteogama*	Rarely cultivated (Colombia) / wild (Colombia, Ecuador), Humid montane forest, 2000–3500 m.	Glabrous to partly pubescent, fruit oval or ovoid, elongated, yellow or bright red, aril scarce to succulent; highly polymorphic.
P. tarminiana Coppens & Barney (curuba India) not classified in a section	Commercial cultivation (Colombia, Ecuador), 2200–3500 m	Slightly pubescent, corolla shorter than the hypanthium, pink, fruit fusiform, yellow.
P. mixta L. (curuba de monte) Section *Tacsonia*	Wild (Venezuela to Bolivia), sometimes collected. Montane forest and disturbed areas, 2000–3500 m.	Glabrous to pubescent, flower erect, corolla pink to red, fruit green to pale yellow, aril scarce; highly polymorphic
P. ampullacea (Mast.) Harms (gulián) Section *Ampullacea*	Wild (central Ecuador). Montane forest, 2000–3500 m.	Stipules linear-lanceolate, bracts free; flower erect, yellow, fruit oval, elongated, the largest fruit in the subgenus.
P. bracteosa Planch. & Lind. ex Tr. & Planch. Section *Tacsoniopsis*	Wild (north-eastern Colombia and Venezuela). Humid montane forest, 2300–3000 m.	Glabrous; flower pinkish orange, bracts free, sepals fused, petals inserted on the sepals, fruit fusiform.
P. pinnatistipula Cav. (tin tin) Section *Poggendorfia*	Homegardens (Colombia to Bolivia) / wild (Peru, Bolivia), 2500–4000 m.	Partly pubescent, stipules pinnatisect, bracts free, floral tube equivalent in length to the corolla, corona simple, filamentous, fruit spherical, greenish.
P. antioquensis Karst. (curuba antioqueña) Section *Colombiana*	Homegardens / wild (Colombia). Humid montane forest, 1800–2700 m.	Stipules linear-lanceolate, bracts free, very long peduncle, floral tube shorter than the red corolla, corona multiple and filamentous, fruit fusiform, green to yellow.
P. manicata (Juss.) Pers. (subgenus *Manicata*)	Wild (Venezuela to Peru). Dry Andean hillsides and disturbed areas, 1500–3000 m.	Flower erect, floral tube shorter than the red corolla, corona multiple and filamentous, fruit ovoid, green.

subgenus *Passiflora*. This flower morphology and the dominance of red in the color of the corolla are adapted to cross-pollination by hummingbirds, and more particularly by the sword-billed hummingbird *Ensifera ensifera* Boissoneau (Trochilidae). Self-incompatibility has been observed in the subgenus *Passiflora* but not in subgenera *Tacsonia* and *Manicata*. The monospecific subgenus *Manicata* is considered intermediate between subgenera *Tacsonia* and *Passiflora*, as the flowers of *P. manicata* (Juss.) Pers. have a tubular hypanthium which is shorter than the sepals and a complex filamentous corona (Coppens d'Eeckenbrugge et al. 1997). Species of the subgenus *Tacsonia* are often considered interfertile, as specialists in their taxonomy have reported many natural hybrids. Artificial hybrids have been easily obtained, even between *P. manicata* and *P. tripartita* var. *mollissima* (Escobar 1985) or *P. tarminiana* (C.I. Medina, personal communication).

The research presented here was aimed at studying isozyme divergence among the most widespread species of the subgenus *Tacsonia*, including *P. tripartita* var. *mollissima* ('curuba de Castilla'), *P. tarminiana* ('curuba india'), *P. cumbalensis* (Karst.) Harms (the rosy passion fruit), *P. mixta* L. ('curuba de indio'), and *P. pinnatistipula* Cav. ('tintin'). The first two are cultivated at a commercial scale by small holders in the tropical Andean highlands (above 2300 m) around the main urban centers where their pulp is used for preparations such as juices, sherbets and ice creams. The others are still common in the wild and/or in home gardens (Fouqué 1972; NRC (National Research Council), Washington, DC 1989). The botanical variety *P. tripartita* var. *tripartita*, as well as some less common species were included in the study. These are *P. antioquensis* Karst. ('curuba antioqueña'), *P. ampullacea* (Mast.) Harms ('gulián'), unique in being a yellow-flowered tacsonia, and *P. bracteosa* Planch. & Lind. ex Tr. & Planch. The widespread *P. manicata*, from the neighbor subgenus *Manicata*, was also included, as well as an accession with the same characteristics except an appreciably longer hypanthium (about the same length as the sepals), classified as *P.* cf. *manicata*. Table 1 gives the infra-subgeneric classification of all these species, as well as their distribution, domestication status and main traits, indicating morphological affinities. Thus, with its relatively short hypanthium and a simple filamentous corona, *P. pinnatistipula* is generally considered intermediate between most species of the subgenus *Tacsonia* and the monospecific subgenus *Manicata*. *P. antioquensis* shows even more similarities with *P. manicata*. Indeed, it was previously included in the subgenus *Granadillastrum* (syn. *Manicata*) (Killip 1938).

Materials and methods

Plant material and enzyme electrophoresis

Plant material consisted of 87 plantlets grown in greenhouse from seeds from 87 different plants. The origins of the material are presented in Table 2 and mapped in Figure 1. As far as possible, the different species were sampled in order to maximize geographic diversity. The accessions were determined in the field according to Escobar (1988), Holm-Nielsen et al. (1988). When possible, the determination was verified after full development of the seedlings. In two cases, morphological differences were observed with the parental material. In the first one (t43), the accession could be classified as *P. tripartita* var. *azuayensis* (pendent light pink flowers with ovate bracts, and glabrous leaves with lanceolate lobes). However, the seedling developed from the collected seeds displayed the linear lobes typical of *P. tripartita* var. *tripartita*. The second case is that of P. cf. *manicata* (e48). Three of the seedlings grown from the fruits did not develop to flower, while the two remaining produced plants with flowers typical of *P. manicata*.

Fifteen enzyme systems were tested (Table 3), and those showing both clear staining and polymorphism on a sample of *P. tripartita* var. *mollissima*, *P. tarminiana*, *P. mixta*, *P. cumbalensis*, and *P. pinnatistipula* were retained. The methodology for isozyme extraction, electrophoresis, and staining developed by Ramírez et al. (1987) was used with the following modifications in the extraction buffer and the starch concentration of the gel. Isozymes were extracted from plantlet leaf tissue in a buffer made of Trizma 0.05 M, DTT 0.005 M, PVP-40 3%, Sorbitol 20% in a 1:2 proportion (weight to volume). In the case of starch systems, the homogenate was absorbed on 0.2 × 1.0 cm chromatographic paper (Watman 3 MM CHR) and loaded into 12% starch gels (Sigma Chemical Co.) previously prepared in histidine-citrate gel buffer and cooled to 4 °C. Samples were electrophoresed in a refrigerator for 6 to 7 h at 300 V and 45 mA. The gels were stained, fixed and stored according to the methodology compiled in (1988). For acrylamide systems, about 300 mg of leaf tissue were macerated

Table 2. Geographic origin of the accessions.

Code	Country	Locality	No. Plants
P. tripartita var. *mollisima*			
mn1	Colombia	Nuevo Colón, Boyacá	1
mn4	Colombia	Subachoque, Cundinamarca	1
mc8	Colombia	Tenerife, Valle del Cauca	1
ms10	Colombia	Pasto, Nariño	1
ms11	Ecuador	Ambato, Tungurahua	1
P. tripartita var. *tripartita*			
t43	Ecuador	Baños, Tungurahua	2
P. tarminiana			
in21	Venezuela	Fruits from Táchira state	1
ic16	Colombia	Tenerife, Valle del Cauca	1
is19	Colombia	Santa Clara, Nariño	1
is20	Ecuador	Ambato, Tungurahua	1
is21	Ecuador	Loja, Loja	1
P. triaprtita var. *mollissima* x *P. tarminiana* (F2)			
h42	Colombia	Pasto, Nariño	2
P. mixta			
xs22	Colombia	Cerrito, Santander	1
xn23	Colombia	Alto del Sote, Boyacá	1
xc27	Colombia	Barragán, Valle del Cauca	1
xs30	Ecuador	Ambato, Tungurahua	1
xs31	Ecuador	Baños, Tungurahua	1
P. cumbalensis			
u32	Colombia	Cumbita, Boyacá	5
u33	Colombia	Paipa, Boyacá	9
u34	Colombia	Nuevo Colón, Boyacá	1
u35	Ecuador	Ambato, Tungurahua	1
P. pinnatistipula			
p36	Colombia	Tuta, Boyacá	12
p37	Colombia	Nuevo Colón, Boyacá	2
p38	Ecuador	Ambato, Tungurahua	17
P. antioquensis			
q39	Colombia	Sta Rosa, Antioquia	2
P. ampullaceal			
1140	Ecuador	Joyacshi, Chimborazo	2
P. bracteosa			
b41	Colombia	Bucaramanga, Santander	1
P. manicata			
a44	Colombia	Chitagá, Norte de santander	2
a45	Colombia	Concepción, Santander	5
a46	Colombia	Nuevo Colón, Boyacá	2
a47	Ecuador	Baños, Tungurahua	2
P. cf. *manicata*			
e48	Colombia	Barragán, Valle del Cauca	5

with the same extraction buffer, in a 1:2 proportion (weight to volume). Samples were centrifuged for 20 min. at 14 000 rpm in an Epperdorf microcentrifuge. The supernatant (25 μl) was electrophoresed on polyacrylamide 4% in the concentration and 10% in the separation gel. The electrophoretic separation was initiated with 30 mA, 70 V, and 1–3 W, and amperage was slowly raised to 50 mA after the tagging dye had passed to the separation gel. The power supply was programmed to maximum values of 250 V and 30 W during separation, which lasted about seven hours. The gels were stained, fixed, and stored according to the methodology compiled in (1988).

Data analysis

The electromorphs (bands) obtained for the six enzyme systems were used as binary descriptors. The

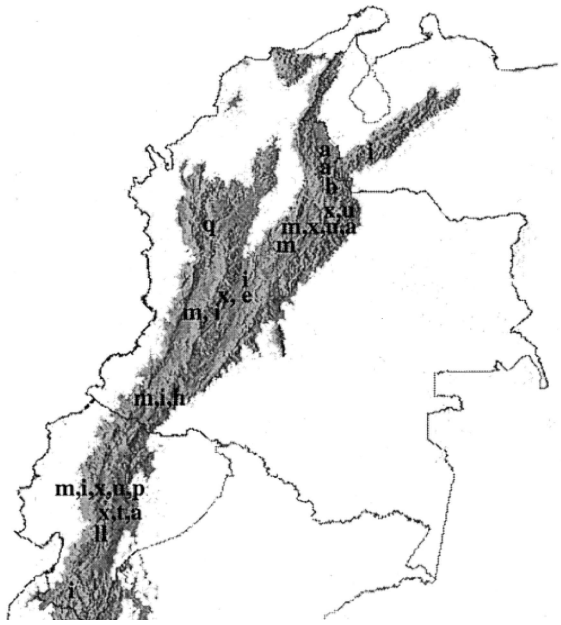

Figure 1. Approximate locations of the accessions used in the study in Venezuela Colombia, and Ecuador m : *P. tripartita* var. *mollissima*; t: *P. tripartita* var. *tripartita*; i: *P. tarminiana*; x : *P. mixta*; u : *P. cumbalensis*; p : *P. pinnatistipula*; q : *P. antioquensis*; II : *P. ampullacea*; b : *P. bracteosa*; h : *P. tripartita* var. *mollissima* × *P. tarminiana*; a : *P. manicata*; e : *P.* cf. *Manicata*.

bands of each system were numbered in the order of cathodal-anodal migration. Individuals were scored for presence or absence of each electromorph. The individuals were grouped by zymotype. If two individuals differed by at least one electromorph they were considered as two different zymotypes. Relationships among the zymotypes were examined by cluster analysis. Jaccard's coefficient of similarity was computed for all possible pair-wise comparisons of zymotypes in the zymotype x electromorph matrix. The distance matrix was presented as an un-rooted dendrogram using the neighbor joining method. All computations were performed using the DARWIN multivariate analysis software (Perrier and Jacquemoud-Collet 1999).

Results

Of the 15 enzyme systems tested, 12 showed clear staining (Table 3), eight of which revealed polymorphism: isocitrate dehydrogenase (IDH), 6-phosphogluconate dehydrogenase (PGD), phosphoglucomutase (PGM) in starch and esterase (EST), Aspartate Aminotransferase (AAT), diaphorase (DIA), peroxidase (PRX), and acid phosphatase (ACP) in acrylamide. However, EST was poorly resolved or inconsistent and AAT exhibited complex banding patterns with six partially overlapping electromorphs, some of which could not always be reproduced. Hence, they were excluded from the analysis. Zymotypes obtained from the six remaining enzyme systems are gathered in Table 4, and examples of gels shown in Figure 2.

Isocitrate dehydrogenase (IDH)

One activity region was revealed with four bands appearing in five patterns. Band 1 is characteristic of *P. tripartita*, *P. tarminiana*, and *P. mixta*. It is also present in *P. antioquensis* and in the Ecuadorian

Table 3. Systems and buffers used to study isoenzyme diversity in 12 taxa of *Passiflora* subgenera *Tacsonia* and *Manicata*.

Enzyme	Abbreviation	E.C.designation	Medium	Staining[2]	Polymorphism[2]
Acid Phosphatase	ACP	3.1.3.2	polyacrylamide	**	*
Alcohol Dehydrogenase	ADH	1.1.1.1	starch	*	-
Diaphorase	DIA	1.6.4.1	polyacrylamide	**	**
Esterase	EST	3.1.1	polyacrylamide	*	*
Glucose 6-Phosphate Dehydrogenase	G-6PDH	1.1.1.49	starch	-	-
Isocitrate Dehydrogenase	IDH	1.1.1.42	starch	**	**
Malate Dehydrogenase	MDH	1.1.1.37	starch	*	-
Peroxidase	PRX	1.11.1.7	polyacrylamide	**	**
Phosphoglucomutase	PGM	5.4.2.2	starch	**	**
6-Phosphogluconate Dehydrogenase	PGD	1.1.1.43	starch	**	**
Shikimate Dehydrogenase	SKDH	1.1.1.25	starch	*	-
Aspartate aminotransferase	AAT	2.6.1.1	polyacrylamide	**	**
Malic Enzyme	ME	1.1.1.40	starch	*	-
Phosphoglucoisomerase	PGI	5.1.3.9	starch	-	-
Glutamate Dehydrogenase	GDH	1.4.1.2	starch	-	-

[2] -: poor-; *: acceptable; **: excellent

Table 4. Zymotypes observed in 12 taxa of subgenera *Tacsonia* and *Manicata*.

Isozyme systems							Accessions (plt number)
IDH	PGD	PGM1	PGM2	DIA	PRX	ACP	
P. tripartita var. *mollissima*							
1	4	5	8	2	2	2	mn01
1	4	5	7	2	2	2	mn04
1	4	5	8	2	2	2	mc08 (a)
1	4,6	5	8	3	2	2	ms10
1	1,3,4,6	5	8	2	2	3	ms11
P. tripartita var. *tripartita*							
1	4	5	8	2,3	2	2	t43
P. tarminiana							
1	4,6	3	8	3	2	2	in12
1	4,6	3	8	3	2	2	ic16
1	4,5,6	3	8	2	2	2	is19
1	4,6	3	8	2	2	2	is20
1	4,7	3	8	3	2	2	is21
P. triaprtita var. *mollissima* x *P. tarminiana* (F2)							
1	4,6	3	6	2,3	2	2	h42
P. mixta							
1	4	5	6	2	2	2	xn22 (a)
1	4	2	7	2,3	2	2	xn23
1	4	3	7	2	2	2	xc27
1	1,4,6	5	6	2,3	2	3	xs30
1	1,3,4,6	3,5	6	2	2	3	xs31
P. cumbalensis							
2,3	2,6	4	7	3	3	2	u33(9), u32(1),u34(1)
2,3	1,2,4,6	4	7	3	3	2	u32(3)
2,3	1,2,4,6	4	7	3	2,3	2	u32(1)
1,3	4,6	4	8	3	2,3	2	u35(1)
P. pinnatistipula							
2	5	5	6	2	1	3	p36(12)
2	5	5	6,8	2	2	3	p37(2)
2	5	5	8	2	1	3	p38(17)
P. bracteosa							
4	7	5	8	1	3	1	b41(1)
P. ampullacea							
2	5	3	8	3	3	3	1140(1)
2	5	3	8	2,3	3	2	1140(1)
P. antioquensis							
1	5	5	6	4	1	4	q39(2)
P. manicata							
2	3,5	5	8	2,5	3	3	a44(2)
2	3,5	5	8	2,5	3	2	a45(1)
2	3,5	5	8	2,5	2	2	a45(4)
2	5	5	8	2,5	3	3	a46(2)
2	4,5,7	5	7	2,5	3	3	a47(1)
P. cf. *manicata*							
2	4,5,7	5	8	2,5	3	3	e48(5)

accession of *P. cumbalensis*. Band 2 is present in all the other accessions, except that of *P. bracteosa*, i.e. in *P. cumbalensis* from Colombia, *P. ampullacea*, *P. pinnatistipula*, *P. manicata*, and *P.* cf. *manicata*. In addition to band 1 or 2, *P. cumbalensis* accessions present band 3. Band 4 is only present in the *P. bracteosa* accession.

6-Phosphogluconate dehydrogenase (PGD)

With 11 different patterns and seven distinct bands, this was the most variable enzyme system. At the interspecific level, it separates *P. tripartita*, *P. tarminiana*, *P. mixta*, and *P. cumbalensis*, characterized by band 4, from the other species (*P. pinnatistipula*, *P.*

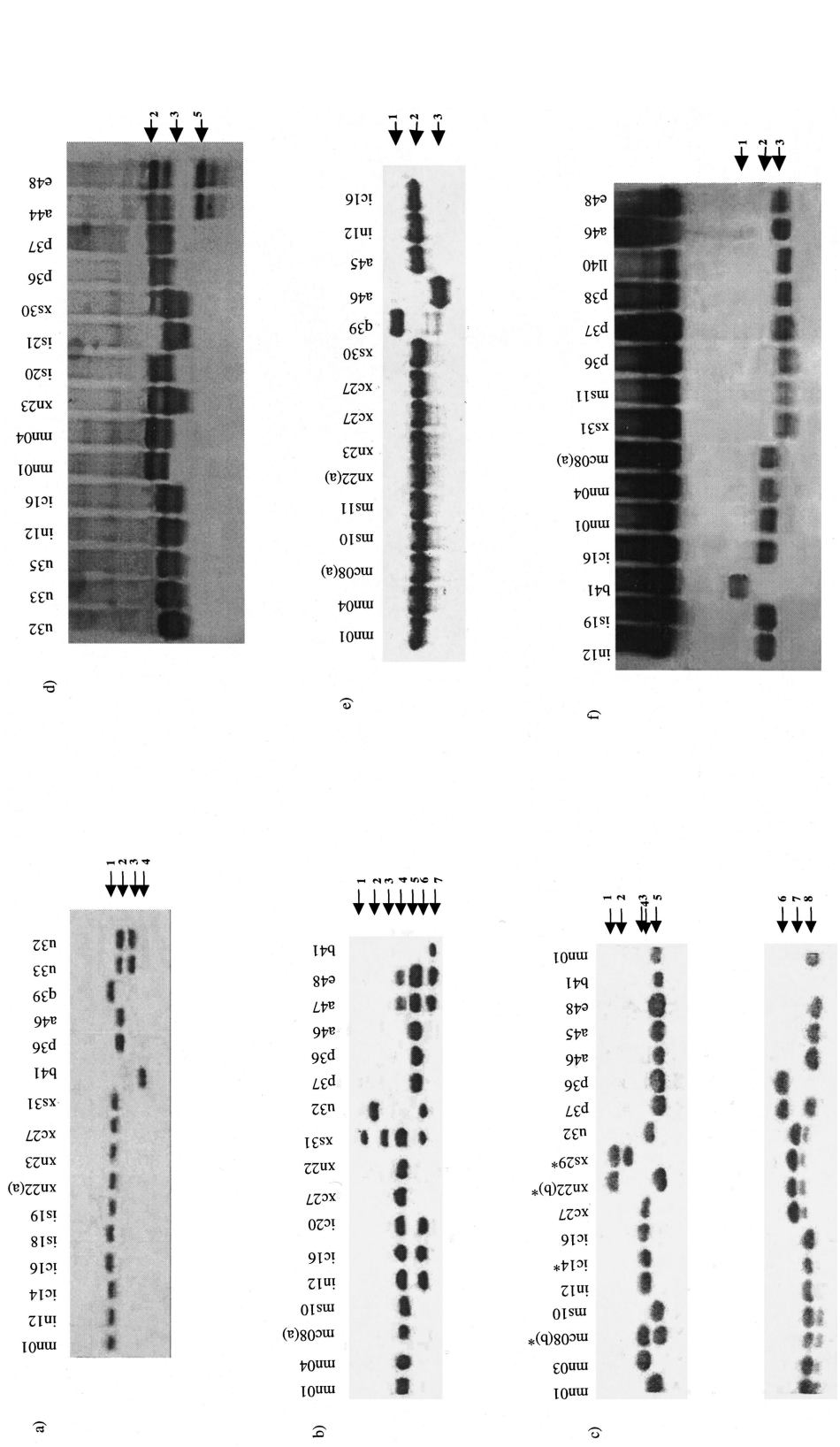

Figure 2. Polymorphism observed for isozyme systems. a: IDH; b: PGD; c: PGM; d: DIA; e: PRX; f: ACP. Arrows indicate band levels as in Table 3. *Individuals not included in the analysis.

bracteosa, *P. ampullacea*, *P. antioquensis*, and *P. manicata*), characterized by bands 5 and/or 7. The only exceptions are the absence of band 4 in one accession of *P. cumbalensis*, its presence in two accessions of *P. manicata* and *P.* cf. *manicata*, and the presence of band 5 in one accession of *P. tarminiana*. The accessions of *P. tarminiana* and *P. cumbalensis* are further characterized by band 6. This band is also present in some accessions of *P. tripartita* var. *mollissima* and *P. mixta*, and in the hybrid h42. Band 1 is found in the most complex zymotypes of *P. tripartita* var. *mollissima*, *P. mixta*, and *P. cumbalensis*. Band 3 is only observed in certain zymotypes of *P. tripartita* var. *mollissima*, *P. mixta*, and *P. manicata*. Band 2 is only observed in 15 individuals of *P. cumbalensis*, all from Colombia. Band 7 is only found in *P. bracteosa* and in two accessions of *P. manicata* and *P.* cf. *manicata*.

Phosphoglucomutase (PGM)

Two distinct regions of staining are observed in all accessions; the higher region (slower migration) exhibits greater activity with five bands and five patterns, the lower region (faster migration) shows three bands and four patterns.

In the first region (PGM1), intraspecific polymorphism is limited to *P. mixta*. Indeed, all accessions of *P. tripartita*, *P. pinnatistipula*, *P. bracteosa*, *P. antioquensis*, and *P. manicata*, exhibit band 5, those of *P. tarminiana* and *P. ampullacea* exhibit band 3, and *P. cumbalensis* diverges in having band 4. *P. mixta* possesses both bands, plus the rare band 2.

For the second region (PGM2), band 8 is the most frequent. It is present in all accessions of *P. tarminiana*, *P. bracteosa*, and *P. ampullacea*, and in most accessions of *P. tripartita*, *P. pinnatistipula* and *P.*

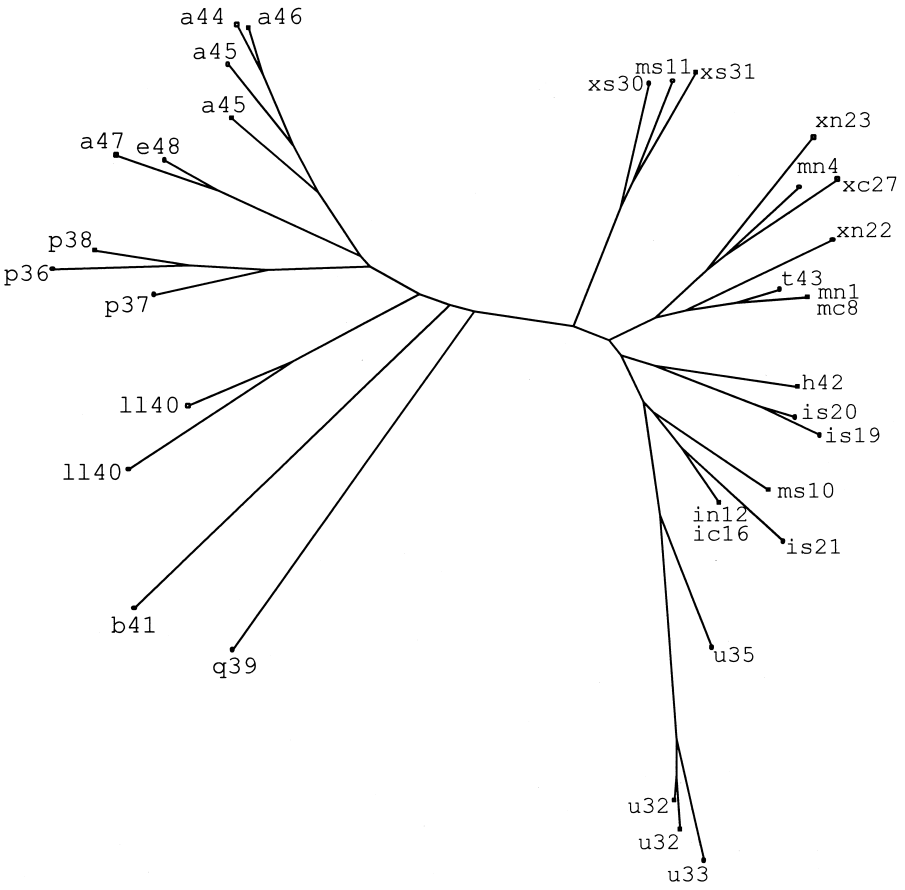

Figure 3. Radial tree resulting from neighbor joining cluster analysis (Jacquard distance). Accessions labels as in Table 2.

manicata. But it is absent in *P. mixta* and in all accessions of *P. cumbalensis* but the one from Ecuador. In these two species, band 7 is the most frequent. Band 8 is also present in one accession of *P. manicata*. Band 6 is only found in two accessions of *P. mixta*, two of *P. pinnatistipula*, and in the accession of *P. antioquensis*.

Diaphorase (DIA)

Gels stained for DIA displayed two zones of activity. As the slow migrating zone was invariant and exhibited a weaker activity, it was not included in the analysis. The more cathodal zone exhibited five bands and six patterns. Band 2 and 3 are the most frequent in the whole sample. Both are found in *P. tripartita*, *P. tarminiana*, *P. mixta*, and *P. ampullacea*. The latter is present in all the accessions of *P. cumbalensis*, *P. pinnatistipula*, and *P. manicata*. *P. manicata* is differentiated by band 5, which accompanies band 3, while *P. bracteosa* and *P. antioquensis* are differentiated by bands 1 and 4 respectively.

Peroxydase (PRX)

Band revelation was particularly clear for this enzyme system. Three bands and four patterns are recognized. Band 2 is characteristic of *P. tripartita* and *P. tarminiana*, their presumed hybrid, and *P. mixta*. It is present at lower frequencies in other species, as in *P. cumbalensis*, *P. pinnatistipula*, and *P. manicata*, where band 3 seems dominant. Band 1 is only found in *P. pinnatistipula* and in *P. antioquensis*.

Acid phosphatase (ACP)

Bands were observed at four different levels. Band 2 is dominant in *P. tripartita*, *P. tarminiana*, *P. mixta*, and *P. cumbalensis*. Band 3 is common in *P. pinnatistipula* (all plants), *P. manicata* and *P.* cf. *manicata* (all five plants). It is also present in *P. tripartita* var. *mollissima*, *P. mixta*, and *P. ampullacea*. Band 1 differentiates *P. bracteosa* and band 4 *P. antioquensis*.

Intraspecific variation

The two cultigens *P. tripartita* var. *mollissima* and *P. tarminiana* showed limited variation for most systems. Particular band combinations were observed for PGD in the accessions of *P. tripartita* var. *mollissima* from southern Colombia and Ecuador. However, the zymotype of the Ecuadorian *P. tripartita* var. *tripartita* is very similar to those observed in the material cultivated in central Colombia. Variation is also limited in the cultivated accessions of *P. cumbalensis* and *P. pinnatistipula*, where zymotypes are very similar and all or most plants from a same accession share the same zymotype. However, the wild Ecuadorian accession of *P. cumbalensis* shows some divergence from the cultivated Colombian types. A similar situation is observed in the wild *P. manicata*, where the Ecuadorian accession diverges in PGD and PGM2. In contrast, the wild *P. mixta* shows wide variation, particularly for PGD and PGM. Small numbers do not allow a comparison with *P. bracteosa*, *P. ampullacea*, and *P. antioquensis*.

Interspecific variation and cluster analysis

No zymotype is common to two species. The distribution of bands often follows a clear interspecific structure. *P. tarminiana*, *P. tripartita* and *P. mixta* share the band IDH-1, and these species plus *P. cumbalensis* share bands PGD-4 and PRX-2. Several species characteristically possess alleles rare or absent in other species. Thus, *P. cumbalensis* possesses PGM1-4, *P. manicata* DIA-5, *P. antioquensis* DIA-4, PRX-1, and ACP-4, and *P. bracteosa* IDH-4, PGD-7, DIA-1, and ACP-1.

The dendrogram obtained from the Neighbor-Joining cluster analysis (Figure 3) clearly separates a first main group composed of the most common and typical species of the subgenus *Tacsonia* (*P. tarminiana*, *P. tripartita*, *P. mixta*, and *P. cumbalensis*) from a second main group constituted by the other species. In the first main group, *P. cumbalensis* is the most clearly differentiated. It forms a distant cluster where the Ecuadorian accession is well separated from the Colombian ones. *P. tarminiana* forms two neighboring clusters, one of which includes an Ecuadorian accession of *P. tripartita* var. *mollissima*. *P. tripartita* and *P. mixta* are not clearly separated and form two clusters whose composition seems to follow a geographic rather than a taxonomic pattern, the largest cluster grouping Colombian accessions of *P. tripartita* var. *mollissima* and *P. mixta*, but also *P. tripartita* var. *tripartita* from Ecuador, and the smaller one grouping three Ecuadorian accessions of *P. tripartita* var. *mollissima* and *P. mixta*. In the second main group, *P. manicata* and *P. pinnatistipula* form two pure clusters at the other end of the dendrogram. The *P. manicata* cluster includes *P.* cf. *manicata* and

shows some divergence between the unique accession from Ecuador and those from northeastern Colombia. *P. antioquensis*, *P. bracteosa*, and *P. ampullacea* form small, distant clusters branching between *P. manicata*/*P. pinnatistipula* and the more typical tacsonias.

Discussion

The high isozyme variation observed in the wild *P. mixta*, as compared to the variation in the cultivated accessions of *P. tripartita* var. *mollissima* and *P. tarminiana*, is fully consistent with the particularly high morphological variability often reported in this species (Killip 1938; Escobar 1988; Holm-Nielsen et al. 1988). A similar range of morphological variability has been reported for *P. cumbalensis*, but the variation in our sample, dominated by cultivated accessions collected North of Bogota, could not reflect the variability of this last species. The limited variation found in *P. cumbalensis* is probably due to endogamy resulting from the very limited size of the cultivated populations and the multiplication system used by the growers (orchards are often established from seeds of a single fruit). The relatively low level of variation in *P. manicata* is more surprising. This species is self-compatible and spontaneously self-pollinated in absence of pollinators, which should favor low within-population diversity but high divergence between populations (Schoen and Brown 1991). Only the atypical accession of central Colombia *P.* cf. *manicata*) and the accession from Ecuador appeared relatively distinct from those of northern Colombia.

In *P. mixta*, *P. tripartita*, *P. cumbalensis*, and *P. manicata*, the structure of intraspecific variation suggested a divergence between Colombian and Ecuadorian accessions. However, this appeared clearly only in the first two species, which showed a geographic structure stronger than the interspecific divergence. This weak differentiation between *P. mixta* and *P. tripartita* var. *mollissima* is consistent with the results of a previous morphological study (Villacis et al. 1998). Indeed, the range of morphological variation in *P. mixta* encompasses the range of variation in *P. tripartita*, the most distinctive trait of *P. mixta* being its partially erect flower. Thus, both morphological and isozyme descriptors suggest a much closer proximity between these two species than would appear from their classification in two different sections of the subgenus *Tacsonia* (Escobar 1988). The two species are interfertile (Escobar 1981; Schoeniger 1986) and could exchange genes easily. The inclusion of one zymotype of *P. tripartita* var. *mollissima* in a cluster including two zymotypes of *P. tarminiana* also suggests the possibility of gene flow between the two cultigens, which are also interfertile (Coppens d'Eeckenbrugge et al. 2001). The relative importance of these genetic exchanges is an essential question for the definition of strategies for the conservation and utilization of banana passion fruit genetic resource. It justified a further study on a wider sample, to be published in a next paper.

In our dendrogram, the most typical (long floral tube, reduced corona) and common species of the subgenus *Tacsonia* (*P. mixta*, *P. tripartita*, *P. tarminiana*, and *P. cumbalensis*) form a first series of clusters, clearly separated from the other, less typical species. This is consistent with RAPD and chloroplastic RFLP data on 14 species from seven subgenera published by Fajardo et al. (1998), Sánchez et al. (1999). With these markers, *P. tripartita* var. *mollissima* and *P. tarminiana* showed limited variation and clustered close to each other, *P. cumbalensis* coming next, while *P. pinnatistipula* and *P. antioquensis* appeared more distant. The results of our cluster analysis are also consistent with the morphological study of Villacis et al. (1998), with *P. manicata* and *P. pinnatistipula* well separated from the four common species, and *P. cumbalensis* at some distance from *P. mixta*, *P. tripartita* var. *mollissima*, and *P. tarminiana*. Indeed, the separation between these four species and the others are paralleled by morphological divergences. *P. ampullacea* possesses characteristic yellow flowers, *P. pinnatistipula* an hypantium of about the same length as the corolla and a simple filamentous corona, *P. bracteosa* petals inserted on the sepals and a verrucose fruit, and *P. antioquensis* and *P. manicata* a short hypantium and a complex corona of short filaments. The position of *P. antioquensis* in the dendrogram suggests that this species is better classified in the subgenus *Tacsonia*, together with other Colombian species with an extremely long peduncle (Escobar 1988), than it was in the subgenus *Granadillastrum* (syn. *Manicata*; Killip (1938)). On the other hand, the typical *P. cumbalensis*, *P. tarminiana*, *P. tripartita*, and *P. mixta* are not more distant from *P. manicata* than from the other species of subgenus *Tacsonia*, which questions the classification of *P. manicata* in a distinct, monospecific subgenus.

Conclusion

The present paper constitutes the first report of iso-

zyme variation in nine species of the subgenera *Tacsonia* and *Manicata*. Six isozyme systems produced consistent results concerning interspecific relationships, separating clearly the accessions of *P. tarminiana*, *P. tripartita*, *P. mixta*, and *P. cumbalensis* from less typical species of subgenus *Tacsonia*. *P. mixta* showed the highest intraspecific variation and the closest affinity with *P. tripartita*. The two species could not be distinguished clearly by their zymotypes, as their accessions mostly clustered according to geographic origin. One of the *P. tripartita* var. *mollissima* accessions clustered close to the *P. tarminiana* accessions. The probable gene flow between the two interfertile cultigens, *P. tarminiana* and *P. tripartita* var. *mollissima*, and the wild *P. mixta* is of particular interest for banana passion fruit germplasm management and breeding, justifying a further more detailed study of the three species with the same isozyme markers.

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Passiflora tarminiana, a New Cultivated Species of *Passiflora* subgenus *Tacsonia* (Passifloraceae)

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ABSTRACT. The new species *Passiflora tarminiana* differs from its closest relative by the character combination of very small acicular stipules and large reflexed petals and sepals. This species has escaped detection despite being widely cultivated in South America. Naturalized populations, particularly in Hawai'i, have created problems for conservation of the native flora. In Colombia it is more frequently adopted in industrial cultivation because of its unusual vigor and resistance to fungal diseases.

RESUMEN. La nueva especie *Passiflora tarminiana* difiere de su pariente más cercano por la combinación de caracteres de las estípulas aciculares muy pequeñas y los pétalos y sépalos grandes y reflexos. Esta especie ha escapado su descubrimiento a pesar de estar extensamente cultivada en América del Sur. Las poblaciones naturalizadas, particularmente en Hawai, han creado problemas para la conservación de la flora nativa. En Colombia se adopta mas frecuentemente en el cultivo industrial debido a su extremo vigor y resistencia a las enfermedades causadas por hongos.

Key words: Hawaii, *Passiflora*, Passifloraceae, South America, tropical fruit.

Passifloras of the subgenus *Tacsonia* are cultivated by many small farmers, from Venezuela to Bolivia. Some species are cultivated in New Zealand (Young, 1970). The main cultivated species was earlier known as *Passiflora mollissima* (Kunth) Bailey (Escobar, 1980, 1988; Jaramillo, 1957), but which we now prefer to recognize as *P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & P. Jørgensen as supported by analysis of morphological (Holm-Nielsen et al., 1988; Villacis et al., 1998) and genetic character states (Fajardo et al., 1998; Sánchez et al., 1999). It is called "curuba de Castilla" in Colombia, "tacso de Castilla" in Ecuador, and "banana passion fruit" in English-speaking countries. The second species of importance in the Andes is "curuba india," "curuba ecuatoriana," or "curuba quiteña" in Colombia, called "tacso amarillo" in Ecuador (Pérez Arbeláez, 1978; A.A.A., 1992; Campos, 1992), and "banana liliko'i" or "banana poka" where introduced in Hawai'i (La Rosa, 1984). It is most frequently found in private gardens, but some commercial growers have, because of its wild-type vigor, started to grow it instead of the "curuba de Castilla," *P. tripartita* var. *mollissima*. We describe this overlooked cultigen as a new species under the name *Passiflora tarminiana*, in recognition of Tarmín Campos (b. 1947), a Colombian agronomist and professor who has contributed enthusiastically for the past 20 years to the development of banana passion fruit cultivation and introduced the first author to the cultivated passifloras of the central Colombian highlands.

Producers and consumers easily differentiate *Passiflora tarminiana* from *P. tripartita* var. *mollissima*, but it has never been mentioned as a distinct species in taxonomical studies. In a letter to Tarmín Campos, Linda de Escobar considered it to be a hybrid of *P. tripartita* var. *mollissima*, possibly with the relatively glabrous *P. cumbalensis* (H. Karsten) Harms (in litt., 28 June 1990). The monographer Killip usually referred it to *P. mollissima*, but occasionally annotated specimens (e.g., *MacDaniels 635*) as "a hybrid between *P. mollissima* and some other species of the *Tacsonia* group." Green (1972: 556) suggested that it be "best treated as a part of the variable *P. mixta* [complex]." The new species has been described as a cultivar in Hawai'i, *P. mollissima* 'Banana Poka' (Grierson & Green, 1996). They considered it a probable hybrid, suggesting that it is not *P. mollissima* but that "it now seems probable that it arose in the wild by introgressive hybridization between this species and some other" (Grierson & Green, 1996: 92–93, pl.). We have observed *P. tarminiana* almost everywhere in the Colombian highlands, as well as in the Andes of Venezuela, southern Ecuador, and Peru, consistently with distinct phenotypic traits (see Table 1). Plants grown from seeds show no segregation for these phenotypic traits, which would not be the case with a hybrid. Recent morphological and

Table 1. Morphological comparison of three common or cultivated species of *Passiflora* subg. *Tacsonia*. Lettered numbers refer to the *R.H.S. Colour Chart* (1966).

	P. tarminiana	*P. tripartita*	*P. mixta*
Stem	Terete	Terete	Sub 5-angular
Leaf pubescence	Absent or nearly so on upper surface, moderate on lower surface	Var. *mollissima*: dense on both sides; other varieties: variable, often glabrous at least on upper surface	Absent on upper surface, often absent to rarely dense on lower surface
Stipules	Small (4–7 mm long, 2–3 mm wide), subreniform, denticulate or serrulate, deciduous	Medium (6–12 mm long, 13–19 mm wide), reniform, serrulate to serrate, persistent	Medium to large (6–20 mm long, 12–30 mm wide), reniform, dentate or serrate, persistent
Peduncle	Slender, variable in length, flower pendent	Slender, short, flower pendent	Stout, variable in length, flower half-pendent to erect
Bracts	United ½ their length or more	United ½ their length or more	United ¾ their length or more
Corolla color	Light pink (red-purple group, 57D, 66D, 74D, 75A/B/C), very rarely white	Pink to magenta (red-purple group, 57C/D, 62A, 65A, 66C–D, 68B, 70D for var. *mollissima*, 53B for var. *azuayensis* Holm-Nielsen & Jørgensen, 58B for var. *tripartita*)	Light pink to bright red (most often red/orange-red group, 39A, 42A, 50A, 51B, 52B, 54A, 54B, 55A, also red-purple group in southern Colombia and Ecuador, 63C/D, 75B)
Corolla shape	Corolla reflexed	Corolla campanulate	Corolla campanulate
Floral tube/sepal ratio	Tube/sepal length ratio ca. 1.3–1.6	Tube/sepal length ratio ca. 2.4–3.2	Tube/sepal length ratio ca. 1.6–2.6
Nectary chamber	Appreciably wider than floral tube	Slightly wider than floral tube	Slightly wider than floral tube
Fruits	Pericarp yellow, sometimes orange-tinged; arils orange, succulent	Pericarp pale yellow (var. *mollissima*) to yellow (var. *tripartita*); arils orange, succulent	Pericarp often green at maturity, sometimes turning yellow; arils gray to orange, scant

isozyme studies have confirmed that *P. tarminiana* is distinct from other common species of subgenus *Tacsonia*, such as *P. tripartita* var. *mollissima*, *P. mixta* L.f., *P. cumbalensis*, and *P. pinnatistipula* Cavanilles (Segura et al., 1998; Villacis et al., 1998).

Passiflora tarminiana Coppens & Barney, sp. nov. TYPE: Colombia. Valle del Cauca: Tenerife (municipio El Cerrito), under cultivation, 2200–2600 m, 3°43.189′N, 76°04.482′W, 8 Mar. 1999, *Coppens IPGRI-AM 72* (holotype, COL; isotypes, AAU, AK, BISH, CUZ, GOET, HUA, *IPGRI*, K, MEXU, MO, MYF, QCA, QCNE, TEX, US, VALLE, VEN). Figures 1–3. Table 1.

Passiflora mollissima (Kunth) L. H. Bailey cv. 'Banana Poka' Anon., in Grierson & Green, Hawaiian Florilegium, pp. 92–93, pl. 1996.

Haec species a *P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & P. Jørgensen sepalis et petalis longioribus perpendicularibus vel reflexis; loculo nectarifero majore; stipulis minoribus acicularibus distinguitur.

Liana, stem cylindrical, bark fibrous; internodes 6–12 cm long; indument canescent, soft to the touch. Stipules acicular, auricular, and aristate, 4–7 × 2(–3) mm (1–3 mm long without the aristate apex), arista 3–4 mm long, early deciduous. Petioles 1.5–4 cm, slightly caniculate adaxially, canescent-ferruginous pubescent with 1 to 4 pairs of adaxial glands. Leaves trilobed, (7–)16(–29) cm wide; lobes ovate, acuminate; margin serrate, central lobe (5.5–)11(–16) × (2.5–)5(–8) cm, lateral lobes (5–)9(–16) × (2.3–)4(–7) cm; lamina moderately lustrous above, glabrescent or scarcely pubescent, trichomes mostly short, mixed with some very long; undersurface canescent-pubescent, the trichomes ferruginous along the nerves. Flowers axillary, solitary, pendent; peduncles 3–10 cm, canescent-pubescent; bracts 3–5 × 2–3 cm, united

halfway, margins entire, ovate, acuminate, nerves yellowish, reticulate venation visible, located 1 cm from hypanthium base; floral tube (including hypanthium) 6–8 × 0.7–1 cm, light green outside, whitish inside; nectar chamber semiglobose, 1.4–2 cm wide; operculum reflexed, margin recurved; annulus present; sepals and petals bright pink to light pink, generally 64D or 75A in the *R.H.S. Colour Chart* (1966), one white sport seen, opening perpendicular at anthesis, then becoming reflexed later in the day or on the second day; sepals 4.5–6 × 1.2–2.5 cm, oblong, aristate subterminally, awn 3–4 mm; petals 3–6 mm shorter than the sepals; floral tube/sepal length ratio 1.3–1.6; corona reduced to a tuberculate ring at mouth of floral tube, white with purple base; androgynophore 7–10 cm, white; free staminal filaments 2 cm, white; anthers yellow; ovary fusiform, green, pubescent; styles white, stigmas green. Fruit 10–14 × 3.5–4.5 cm, fusiform; young fruits canescent, the pericarp dark green with white dots except along the main vascular bundles, the dried styles persistent; during maturation dots disappearing and fruit turning yellow to orange yellow. Seeds asymmetrical, reddish brown when dry, reticulate, acute, cordate; arils orange, sweet, and aromatic.

Figure 2 shows the sites where *P. tarminiana* has been observed or collected in the Andes. Table 1 presents a comparison of *P. tarminiana* with two other similar and common species of the subgenus *Tacsonia*. The most typical traits of *P. tarminiana* are the absent or very reduced pubescence on the upper side of the leaves, the minute stipules that are almost always deciduous, the flower with a smaller floral tube/sepal length ratio, as compared to other similar and common species such as *P. tripartita* (Jussieu) Poiret or *P. mixta*. It is further characterized by reflexed light pink petals, a nectar chamber that is much wider than the floral tube, and a fusiform fruit with small whitish dots that are evenly distributed on the pericarp before maturity, except on the six main vascular strands. In comparison, the other widely cultivated banana passion fruit, *P. tripartita* var. *mollissima*, shows a marked pubescence on both leaf sides, persistent and larger stipules, a bell-shaped corolla, a longer floral tube, and shorter sepals and petals. The fruit of the cultigen *P. tripartita* var. *mollissima* is oblong with round extremities, and uniformly green before maturity (however, *P. tripartita* var. *tripartita* may also show whitish dots on the immature fruit). When both cultigens can be compared in the same orchard, *P. tripartita* var. *mollissima* shows much darker foliage, magenta flowers, and pale yellow mature fruits. The fruits of *P. tarminiana* are of a deeper yellow to orange color, and their pulp is less aromatic and tart. These differences in shape and color make them easy to recognize.

According to the botanical keys of Colombia and Ecuador, *P. tarminiana* would key out to species with broadly ovate-reniform or auriculate and denticulate stipules and pendent peduncles, near *P. cumbalensis* and *P. tripartita* (*P. mollissima* in Escobar, 1988). Our new species can easily be distinguished from either of these species by the size and duration of the stipules and the widening of the nectar chamber. Leaf pubescence is not useful to discriminate *P. tarminiana*, as both *P. cumbalensis* and *P. tripartita* show variation for this trait. In Colombia, because *P. tarminiana* had not been described as a distinct species, and because it is sometimes named "curuba quiteña" or "curuba ecuatoriana," some researchers confused it with *P. tripartita* var. *tripartita*, from Ecuador. This confusion is sometimes found in the "gray literature" (research reports and student theses, e.g., Sañudo & Jurado, 1990).

Confusion with *P. tripartita* var. *mollissima* or with supposed hybrids is frequent in the horticultural, weed science, and fruit culture literature. Pictures of flowers and fruits of *P. tarminiana* are frequently presented as those of *P. tripartita* var. *mollissima* (e.g., Vanderplank, 1996; Ulmer & Ulmer, 1997; Wagner et al., 1999). Sorting out these two species is of special concern to biological control of invasive species programs, where host specificity determines which controls may be used and may have broad implications for conservation policy (see Waage et al., 1981; Chacón & Hernandez, 1981).

As commonly observed in the subgenus *Tacsonia*, *P. tarminiana* hybridizes easily with other species of the subgenus. The hybrids with *P. mollissima* and *P. mixta* are fertile and show intermediate phenotypes (Coppen, pers. obs.). Hybrid seeds have also been obtained with *P. cumbalensis* (J. F. Restrepo, pers. comm.).

Passiflora tarminiana is adapted to a wide range of elevations as compared to other species of subgenus *Tacsonia* growing at tropical latitudes. It may be cultivated from about 2000 m up to more than 3000 m. In comparison, *P. tripartita* var. *mollissima* is not well adapted under 2400 m. As in *P. tripartita* var. *mollissima*, the fruits of *P. tarminiana* grow larger at higher elevations. *Passiflora tarminiana* seems to be more resistant to fungi. La Rosa (1984) reported widespread lesions of *Alternaria* and *Coletotrichum* fungi on the fruits in Hawai'i, but we have never observed conidia on its leaves or a sig-

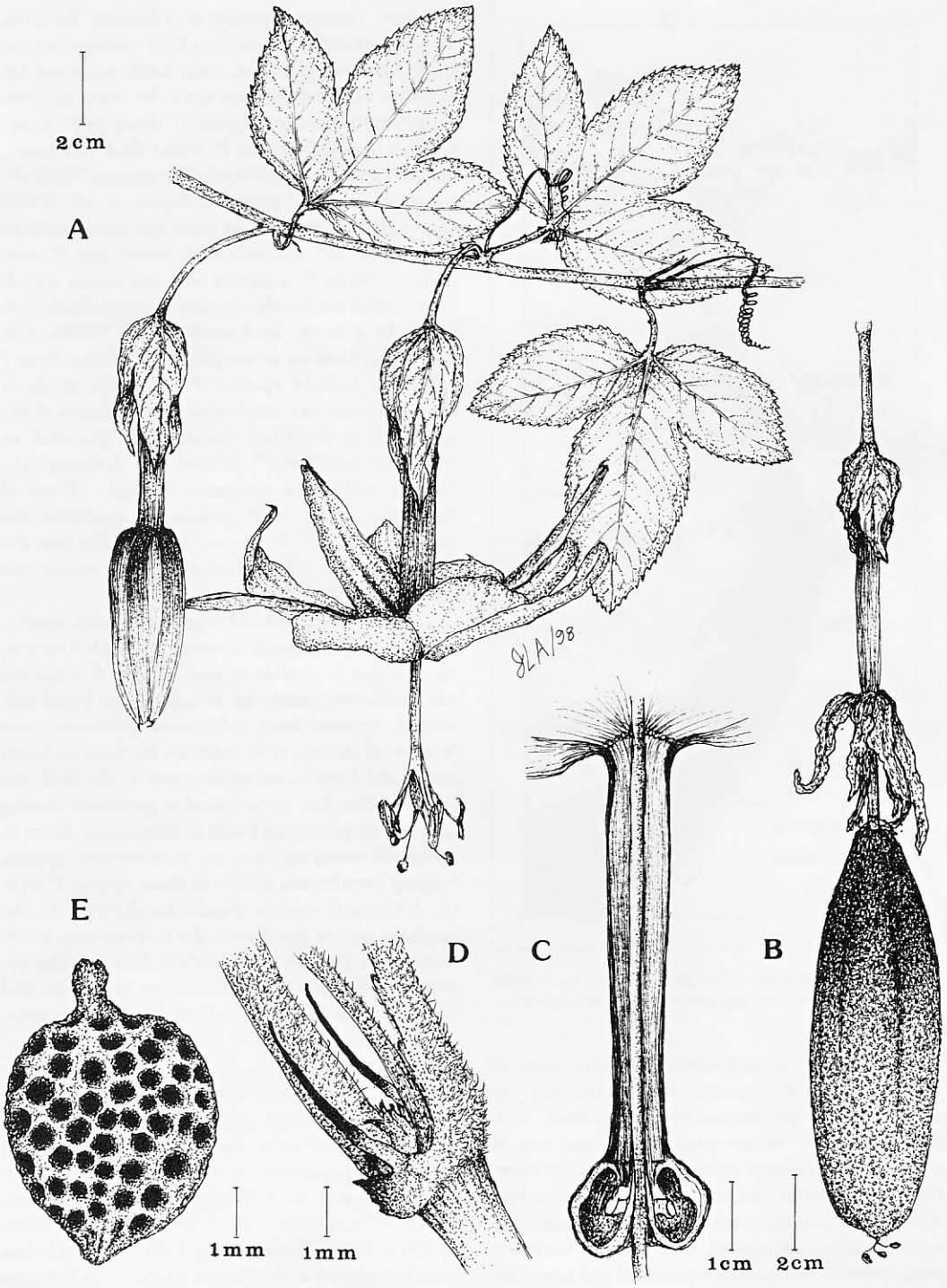

Figure 1. *Passiflora tarminiana* Coppens & Barney. —A. Habit with bud and flower at anthesis. —B. Fruit. —C. Longitudinal section of hypanthium and floral tube showing nectary chamber, operculum, and reduced corona. —D. Node showing stipules. —E. Seed. All drawn from the plants of the type collection.

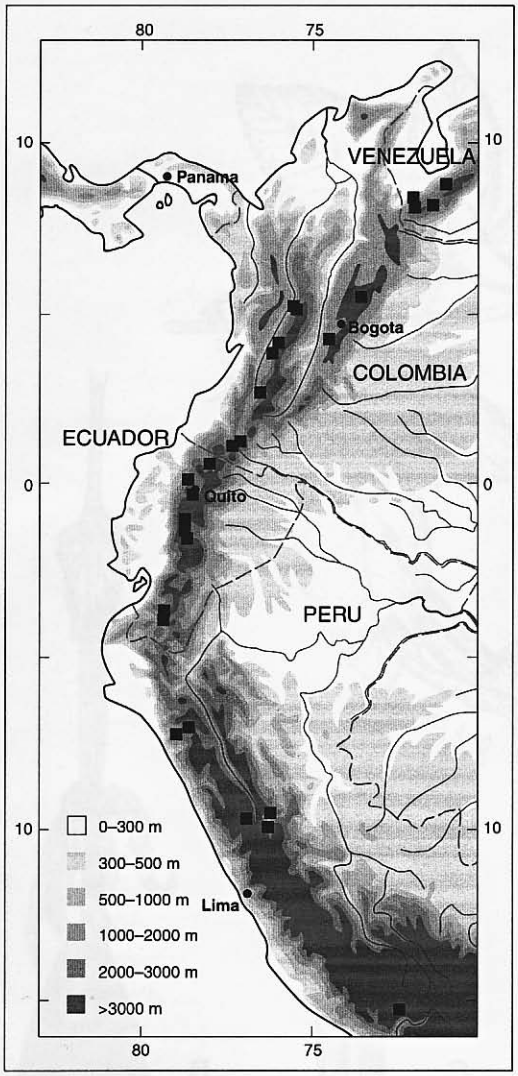

Figure 2. Distribution of *Passiflora tarminiana* in northwestern South America. Squares represent collections.

nificant number of anthracnose necrotic spots on its fruits in South America. On the contrary, the pericarp of *P. tripartita* var. *mollissima* fruits is often affected by anthracnosis, which reduces its market value despite its superior taste. In Venezuela, *P. tripartita* var. *mollissima* has shown high susceptibility to fusarium blight while *P. tarminiana* appeared tolerant or resistant (E. González, pers. comm.). The adaptive potential and rustic nature of *P. tarminiana* have probably been key factors in its conquest of new habitats in New Zealand and Hawai'i where it is reported as a noxious weed (La Rosa, 1984).

Villacis et al. (1998) studied morphological variation in an Ecuadorian field collection including the most common species of subgenus *Tacsonia*. The cluster analyses based on both quantitative and qualitative morphological data clearly separated accessions of *P. tarminiana* from the other species. *Passiflora tarminiana* appeared closer to *P. tripartita* var. *mollissima* and *P. mixta* than to *P. cumbalensis* and *P. pinnatistipula* Cavanilles. Similarly, using six isozyme systems, Segura et al. (1998) showed that *P. tarminiana* is clearly separated from *P. tripartita* var. *mollissima*, *P. mixta*, and *P. cumbalensis*, while *P. tripartita* var. *mollissima* and *P. mixta* could not be clearly distinguished from each other. In a study by Fajardo et al. (1998) with RAPD markers on a sample of 52 plants from 7 subgenera and 14 species of passifloras, 8 plants of *P. tripartita* var. *mollissima* and 5 plants of the species here described (identified in the work as *Passiflora* sp. "india") formed two different subclusters within the subgenus *Tacsonia*. Three of these five plants of *P. tarminiana* produced the same cpDNA RFLP pattern, distinct from that obtained on cpDNA from *P. tripartita* var. *mollissima* (Sánchez et al., 1999).

The exact geographical origin of the new species is obscure. Throughout its range in South America, its situation is similar to that seen in *P. tripartita* var. *mollisima*: plants are nearly always found cultivated, escaped from cultivation, persistent near human habitation, or at least not far from orchards and roads. Despite numerous years in the field, the senior author has never found a specimen coming from a well-preserved forest or subparamo. Even in disturbed areas, we have not seen the new species forming populations similar to those seen in *P. mixta*. Additional studies should be directed to the southern part of the Andes: the isozyme data for *P. tarminiana* (Segura et al., 1998) show a wider diversity in Ecuador than Colombia or Venezuela, and herbarium specimens from Peru seem slightly more morphologically variable.

Passiflora tarminiana has been introduced into numerous cool tropical and tropical montane areas other than its original Andean range, in some cases becoming an invasive weed. Our examination of exsiccatae documents its spread to California by 1907, to Hawai'i by 1921 (La Rosa, 1984), to Mexico by 1936, to Ethiopia by 1967, to New Guinea by 1972, and to Zimbabwe by 1981. It recently has been introduced to the French island of La Réunion at elevations over 700 m (C. Lavigne, pers. comm.).

Most of the paratypes cited below are in small herbaria not registered with *Index Herbariorum*, and their abbreviations are italicized to distinguish them from approved herbarium acronyms. These abbreviations, *INIA*, *INIAP*, *IPGRI*, and *CIRAD-*

Figure 3. Color photos of the type collection plants, *Coppens IPGRI-AM 72*.—A. Habit of flowers, buds, and immature fruits. —B. Longitudinal section of flower showing interior of floral tube and nectary chamber; extra flap of tissue seen on left wall of nectary chamber is an artifact from sectioning. Bracts have been separated for clarity. —C. Shoot tip showing underside of leaves and distally valvate bracts completely enclosing young buds. —D. Mature fruits, one sectioned to show arils and seeds.

FLHOR/IPGRI, correspond to the following institutions: *INIA*—Instituto Nacional de Investigación Agraria, Perú, Casilla 2791, Lima 1, Peru; *INIAP*—Instituto Nacional de Investigaciones Agropecuarias, Ecuador, C.P. 17-01-340, Quito, Ecuador; *IPGRI*—International Plant Genetic Resources Institute, IPGRI-AM, oficina para las Americas c/ o CIAT, A.A. 6713, Cali, Colombia; *CIRAD-FLHOR/IPGRI*—field germplasm collections in Tenerife, Colombia, maintained by CIRAD-FLHOR/IPGRI Project for Neotropical Fruits, address above.

Paratypes. COLOMBIA. **Cauca:** Silvia, *Barney IPGRI-AM-14* (*IPGRI*). **Valle del Cauca:** Barragán, 4°01.52′N, 75°53.54′W, 2900 m, *Coppens & S. Segura IPGRI-AM-3* (*IPGRI*); Tenerife (municipio El Cerrito), under cultivation, 2200–2600 m, 3°43.189′N, 76°04.482′W, same plants as type, *Coppens & Barney IPGRI-AM 2* (*IPGRI,* MO). ECUADOR. **Carchi:** S of Tulcán, 0°30.52′N, 77°54.05′W, 2690 m, *Coppens & Barney IPGRI-AM-13* (*IPGRI*). **Chimborazo:** Volcán Chimborazo, *Barney IPGRI-AM-8* (*IPGRI*); Riobamba, Químiag, 2650 m, *C. Tapia & J. Velásquez CS-070* (*INIAP*). **Loja:** Santiago, 3°47.38′S, 79°17.38′W, 2450 m, *Coppens IPGRI-AM-10* (*IPGRI*); Saraguro, San Lucas, 2550 m, *C. Tapia & E. Morillo CTEM-040* (*INIAP*). **Pichincha:** cultivada, Parroquia Calacali, Reserva Geobotánica Pululahua, 0°05′N, 78°30′W, *Cerón & Cerón 2740* (MO); 0°22′S, 78°25′W, 2650 m, *Coppens & Barney IPGRI-AM-12* (*IPGRI*); Unchibamba, S of Quito, 1°07.85′S, 78°35.32′W, 2610 m, *Coppens & Barney IPGRI-AM-11* (*IPGRI*); Rumiñahui, Iasa, 0°22′S, 78°25′W, 2650 m, *N. Mazón & B. Elizalde NMO-038* (*INIAP*). **Tungurahua:** Ambato, 1°22.02′S, 78°36.21′W, 2500 m, *Barney IPGRI-AM-9* (*IPGRI*); Baños, 2680 m, *Coppens IPGRI-AM-4* (*IPGRI*). PERU. **Arequipa:** Tuhuana, 15°39′06″S, 72°28′09″W, 2545 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 230* (*INIA*). **Cajamarca:** Barrio Santa Elena, 7°17′51″S, 78°51′56″W, 2730 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 170* (*INIA*); alrededores de Guzmango, Prov. Contumazá, 2600–2700 m, *Sagástegui A. 122* (US). **Huánuco:** Chinchao, 9°72′72″S, 76°09′68″W, 2650 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 101* (*INIA*), 2480 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 104* (*INIA*); Soldado Ucro, 9°80′90″S, 76°80′00″W, 3200 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 113* (*INIA*); Conchamarca, 10°03′99″S, 76°20′35″W, 2490 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 116* (*INIA*); La Libertad-Ting, 10°01′56″S, 76°17′00″W, 2820 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 118* (*INIA*); Quiulacocha, 10°01′56″S, 76°17′00″W, 2820 m, *Ll. Rios, J. Medina & L. López INIA-PRONARGEB 120* (*INIA*). VENEZUELA. **Mérida:** Mucuruba, 8°09.46′N, 71°20′W, 2000 m, *E. González & Barney IPGRI-AM-6* (*IPGRI*). **Táchira:** Betania,Villa Paez, 7°31.70′N, 72°26′W, 2000 m, *E. González & Barney IPGRI-AM-5* (*IPGRI*); Pueblo Hondo, 8°15.19′N, 71°53.07′W, 2500 m, *E. González & Barney IPGRI-AM-7* (*IPGRI*).

Representative specimens. ETHIOPIA. Alemaya, cultivated, *Westphal & Westphal-Stevels 494* (MO). MEXICO. **Distrito Federal:** cultivated at El Rosario, *MacDaniels 635* (BH). **Michoacán:** desv. a San José del Rincón carr. Angangeo–Villa Victoria, *Soto & Ramírez 1496* (MEXU, MO). **Morelos:** Mpio. Huitzilac, *H. Hernández 16* (MEXU); Mpio. Huitzilac, 1.2 km de la Carr. Federal Cuernavaca–México, D.F., rumbo a Zempoala, *Luna C. 21* (MEXU, MO). NEW ZEALAND. **North Island:** Mount Albert, *Astridge* (AK-*219103*); Wellington, *Brownsey* (AK-*152731*); Titirangi, *Cameron* (AK-*221386*); Grafton Gully, *Cameron* (AK-*221519*); Waiheke Island, *Cameron 7524* (AK-*229217*); Swanson, *Cameron 9458* (AK-*236385*); Paihia, *Cumber* (AK-*116173*); Mount Albert, *Dingley* (AK-*122719*); Palmerston, *Esler* (AK-*173113*); Mount Albert, *Esler* (AK-*219104*), *Esler* (AK-*219109*); Kerikeri, *Esler* (AK-*219107*); Wood Bay, *Esler* (AK-*219108*); between Nelson City and Whakapuaka, *Healy 74/80* (MO); Waitemata, *Mackinder* (AK-*162676*); Tutukaka and Matapouri, *Newfield* (AK-*212296*); Epsom, *J. Reid* (AK-*116084*); Motuihe, *Sikes* (AK-*220536*); Buller, Karamea, near Karamea, *Sykes 10/85* (MO); Hokianga, *Wright 912* (AK-*138965*); Waitemata, *Wright 1657* (AK-*140997*); Mount Albert, *B. Young* (AK-*114204*), *B. Young* (AK-*114205*), *B. Young* (AK-*116172*), *B. Young* (AK-*117558*); Titirangi, *B. Young* (AK-*116171*), *B. Young* (AK-*117563*); Otahuhu, *G. Young* (AK-*116164*). **South Island:** Port Hills, *Sikes* (AK-*225281*); Punakaiki, *B. Young* (AK-*117584*), *B. Young* (AK-*221387*). PANAMA. **Chiriquí:** carr. hacia la cima del Volcán Barú, *Montenegro 1630* (MO). PAPUA NEW GUINEA. **New Guinea:** Eastern Highlands, Mount Wilhelm near Iwam Pass, *Takeuchi 5898* (MO). U.S.A. **California:** cultivated "in Southern California," *Boughton 242* (US); Golden Gate Park, San Francisco, *Wight 1806* (MO). **Hawaii:** Hwy. 550 along Waimea Canyon, mile 14 near NASA tracking station, *Croat 44833* (MO); Kaua'i, rd. to Kumuwela Lookout, *Crosby & Anderson 1496* (DUKE); Hawai'i, Muana Kea, *Degener et al. 20354* (MO); Kaua'i, near Kokee Ranger Station, *Degener & Degener 35181* (MO); Hawai'i, Puna, Hawai'i Volcano National Park, *Degener & Degener 35183* (MO); Kaua'i, *Henrickson 4034* (NCU); Hawai'i, Puna district, land of Olaa, *D. Horbst* (MYF-*459*); Kaua'i, Waimea District, Na Pali-Kona Forest Reserve, Makaha Valley, *Lorence 5221* (MO); Kaua'i, Pu'u Hinahina Lookout, Waimea Canyon, *Thorne & Zupan 10153* (MO); Hawai'i, Muana Kea road by Douglass Monument, *Trujillo s.n.* (MO); Hawai'i, North Kona, Puuwaawaa, *Webster & Wilbur 1853* (DUKE). ZIMBABWE. Distr. Inyanga, Inyanga Downs, naturalized in Kloof, near sawmill, *Geddes s.n.* (MO).

Numerous germplasm collections of the new species from five departments in Colombia and one in Ecuador are presently maintained at *CIRAD-FLHOR/IPGRI.*

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Table 1. The botanical illustration was executed by Jairo Larahondo Aguilar.

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